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MOVEMENTS, HABITAT SELECTION AND POPULATION STRUCTURE OF BUFFALO (SYNCERUS CAFFER CAFFER SPARRMAN) IN THE SABI SAND WILDTUIN

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MOVEMENTS, HABITAT SELECTION AND POPULATION STRUCTURE OF BUFFALO (*SYNCERUS CAFFER CAFFER* SPARRMAN) IN THE SABI SAND WILDTUIN.

by

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MOVEMENTS, HABITAT SELECTION AND POPULATION STRUCTURE OF BUFFALO (*SYNCERUS CAFFER CAFFER* SPARRMAN) IN THE SABI SAND WILDTUIN.

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ABSTRACT

Buffalo herd movements, home range, habitat selection, herd structure and daily activity patterns where studied for 14 months in the Sabi Sand Wildtuin, Transvaal, South Africa. The structure of the herds remained stable throughout the year with some overlap in home ranges. No subgroups were found to exist in herds. Adult females outnumbered adult males with all other age classes having 1:1 ratios. Bachelor male groups fluctuated seasonally in size, with adult bulls joining the breeding herd in summer in order to mate. The buffalo did not use the available habitat types in proportion to there occurrence, and showed seasonal variation in habitat selection. Movement patterns were adjusted seasonally to accommodate various shifts in habitat selection and water availability. Although the buffalo had certain favoured grazing areas and routes between resource patches they did not show a fixed pattern of range utilization. Buffalo herd movements and seasonal shifts in habitat selection ensured utilization of the most suitable habitat in the various seasons, which were not necessarily the best available. Graze availability and water resources were the main factors that controlled herd movements. Daily activity patterns were adjusted in response to seasonal variation in resource availability and distribution.

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This thesis is dedicated to my parents
Dr. and Mrs. M.R. Funston both of whom have
been unfailing in their support and
love during my studies.

CHAPTER 1: INTRODUCTION

INTRODUCTION

The famous professional hunter, John Hunter (1953) in his book "Hunter" wrote of the buffalo "Many hunters believe that the buffalo is Africa's most dangerous animal. When a buffalo attacks, he charges with admirable ferocity and will not flinch away from a bullet as do rhinos and even elephants. A buffalo usually continues a charge until he is killed or he has killed the hunter". And in the words of hunter/author Peter Hathaway-Capstick (1977) "an angry buff will flatten the unwary hunter flatter than the American dollar after the depression". These are just two of the comments in the popular literature about the never say die strength and cunning determination should the foolhardy hunter wound his quarry.

It is this association with hunting the buffalo that attracts the wealthy trophy hunter and thus makes this species economically important today. It does, however, have even greater importance for the ecology of the veld in African conservation areas. Few populations exist outside the confines of national parks and large private game reserves, and those populations that are conserved are being managed in terms of population growth because of possible impact on the available habitat.

Detailed studies on their ecology and behaviour are limited to those of Grimsdell (1969), Sinclair (1969), Mloszewski (1984), Taylor (1985) and Prins (1987). With the exception of Taylor (1985), the above authors conducted their research in east Africa, while Taylor (1985) studied the response of buffalo to the *Panicum repens* Kariba lakeshore grassland. Buffalo populations in South Africa have been neglected in this respect and the most important contribution to date has been that of Pienaar (1969). Many studies, however, have dealt with the numerical status and population trends in national parks across Africa (Lamprey 1964, Pienaar 1969, Sinclair 1974a, 1974b, 1974c, 1974d, Eltringham & Woodford 1973, Conybeare 1980) and feeding, parasites and disease (Grimsdell & Field 1969, Vesey-Fitzgerald 1969, 1974, Leuthold 1972).

Buffalo populations in conservation areas in southern Africa have increased since they have been protected. However, although the factors controlling these increases in buffalo numbers are not clearly understood, population control measures have been applied. Therefore, studies on the population dynamics of this species in South Africa are urgently required. In particular, baseline information on such aspects as the social organization, social behaviour, spatial organization, activity patterns, resource requirements, feeding ecology and predator-prey relationships should be provided to enable sound management of such populations.

Clutton-Brook & Harvey (1978) have shown that the survival value of the social organization adopted by a given species can only be fully appreciated if it's relationship with food exploitation has been studied. The present thesis reports on the results of field observations collected with a view to formulating a theory on the control of movements by large mammalian herbivores within their range. The results obtained in East African buffaloes (*op cit*) will assist in the formulation.

The key questions of the study, therefore, were:

1) Do herds disperse/aggregate as a function of their habitat utilization?
2) Do herds contain subgroups or social units smaller than the herd?
3) Does the distribution and movement of the herd function to maximize utilization of the best available habitat?
4) Do buffalo herds show a fixed pattern of range utilization?
5) Do buffalo leave a resource patch before it is depleted or trampled?

The buffalo was a natural choice for the study. It was a bonus to find a study area which had a stable buffalo population and access to the study animals through a network of roads and permission to work offroad. The present study, therefore, examines the spatial, temporal and social organization of buffalo and their feeding behaviour in relation to the Sabi Sand Wildtuin environment, and hopefully has application in other similar habitats in southern Africa.

THE AFRICAN BUFFALO (*SYNCERUS CAFFER CAFFER*)

The African buffalo *Syncerus caffer* was first described by Sparrman in 1779 from a type specimen shot along the Sunday's river near Algoa bay (Port Elizabeth) (Allen 1939). The African buffalo is an endemic species of the African continent and is, like the water buffalo, cattle and bison, a member of the family Bovidae. Although recent taxonomists (Ansell 1972, Grubb 1972) consider that there is only one species of buffalo in Africa, they have described a number of subspecies, and clearly there is considerable variation, particularly between East and West Africa. The southern African species is described by Skinner & Smithers (1990) as a large and heavy bovid (body mass range 750-800 kg), with cattle like features. The horns are heavy and widely curved with a massive boss which is less developed in females.

Mating takes place from March to May, followed by a gestation period of 330 days (Kenneth & Ritchie 1953). Calves are born from January to April peaking in January and February (Fairall 1968). Buffalo have a potential longevity of 25 years, but it is doubtful whether wild animals attain an age greater than 20 years (Pienaar 1969).

Buffalo were once distributed over most of Africa south of the Sahara (Sinclair 1977; Skinner *et. al.* 1990). In southern Africa their habitat has become very restricted, and they occurr in significant numbers only in the extreme northeastern parts of Namibia, the northern parts of Botswana, the northern, northeastern and southeastern parts of Zimbabwe, the eastern Transvaal, northeastern Natal and in the Addo Elephant National Park in the Cape Province (Skinner *et. al.* 1990).

Buffalo are found in a wide variety of vegetation types, including the dense lowland forest of the Congo basin, montane forest in East Africa, moist and dry woodlands in central and southern Africa, the *Acacia* grasslands of the Sahel zone in West Africa and the plains of East Africa - in fact, wherever permanent water is found. On some mountains they live at altitudes above 4000 m, where they experience frosts at night, but in West Africa they tolerate high ambient temperatures with high humidity (Sinclair 1977). Stewart & Stewart (1963) state that in East Africa buffalo move into dry scrub in the wet season but they are not found in areas with a mean annual rainfall of less than 250 mm. In short, the species is much more catholic in its habitat choices than other bovids.

The savanna buffalo, *S. c. caffer*, is gregarious, occurring in herds of up to several thousand, whereas forest buffalo (*S. c. nanus*) live in small herds of three's and four's. Leuthold (1972) and Sinclair (1977) report that these large herds are relatively stable, fragmenting into smaller herds when there is ample grazing and water. Large herds tend to show seasonal movements, moving to permanently watered areas in dry periods, and moving out into the rest of their home range in wetter periods (Sinclair 1977).

Sinclair (1977) found that buffalo in East Africa showed regular or seasonal movement, associated with the occupation of different habitats at different times of year. These movements reflect adjustments in meeting resource requirements, especially fluctuations in the availability of food and water. He proposed that the distribution and movement of buffalo function to maximize utilization of the optimum habitat at the height of food scarcity.

Habitat requirements include a plentiful supply of grass, shade and water (Hofmann 1973, Skinner *et. al.* 1990). Hofmann & Stewart (1972) classify buffalo as being bulk and roughage type feeders, more specifically fresh grass grazers dependent on water, characterized by having a capacious rumen. Buffalo feed rather indiscriminately on leaves of grass in the middle herb layer (Field 1968; Bell 1969; Pienaar 1969; Leuthold 1972), and occasionally on the leaves and shoots of forbs, sedges, shrubs and trees (Lamprey 1963; Pienaar 1969; Leuthold 1972). Field (1968) indicates that they show selective avoidance (presumably olfactory) of certain perennial grasses during most of the year, but graze them at the height of the dry season.

Selective overgrazing is avoided, the habitat being utilized in an economical manner, which is probably related to herd movements (Vesey-Fitzgerald 1960; Pienaar 1969; Leuthold 1972). Buffalo herds are not known to linger in trampled or depleted areas, but rather move onto new stands of vegetation (Pienaar 1969; Leuthold 1972). It has been proposed that buffalo are important components of natural veld management because they open up tall grassland for other species that have more restricted feeding habits (Pienaar 1969).

OUTLINE OF THE THESIS

The first requirement was a description of the area in terms of habitat types and the proportion of the area occupied by each type. Each habitat type was described in terms of cover, terrain and the association of plant communities. The second requirement was to describe the pattern of climatic conditions, in particular rainfall and temperature. The reaction of the different vegetation types and consequently herbivore species to rainfall, brings in a temporal component that induces seasonality. The seasonal weather patterns for the Sabi Sand Wildtuin were described after analysing the rainfall and temperature data, kept by the warden over the last ten years. Further climatic information was acquired from the weather station at Skukuza in the Kruger National Park, some 50 km southeast of the study area.

Chapter 3 deals with the techniques used to observe and record data on the study herds and bachelor groups of buffalo. Cardinal to any study on population structure (Chapter 4) and growth trends being the classification of individual buffalo by age, sex and social status; the procedures and herd characteristics are extensively described in Chapter 3. Individual recognition, described in Chapter 3, was used in the monitoring of herd composition and stability and the bachelor and herd male dynamics, discussed in Chapter 4.

Discussion of seasonal habitat selection, distribution movement patterns, home range and daily activity patterns are covered in Chapter 5. The estimates of veld condition, available forage and spatial patterning of the vegetation (Chapter 2) are taken into account in this analysis. Chapter 6 deals with the population dynamics of the population including response to drought conditions, predation and population control measures. Chapter 7 takes a comparative look at southern African buffalo herds with respect to data published from other populations in Africa and the conservation and management of the buffalo in the Sabi Sand Wildtuin. In this chapter the results of the study are brought together to formulate a theory on the control of large mammalian herbivore movements.

CHAPTER 2: SPATIAL PATTERNS OF THE VEGETATION IN THE SSW

INTRODUCTION

In order to undertake a study examining movement patterns, habitat selection and feeding adaptations and habitats a vegetation map of the study area within the Sabi Sand Wildtuin (SSW) was required. One of the objectives being to establish the preference of the buffalo for the different habitat types in the reserve. Although the vegetation of the reserve has been described by Tinley (1979), only a few generalized vegetation types were broadly set out. Habitat choice in herbivores is related to a number of parameters, including forage, surface matter and cover. Characteristics of the terrain are, therefore, important for defining different habitat types. The approach followed was, therefore, to analyse and describe the spatial patterns in the landscape with particular emphasis on the vegetation. This has resulted in a 1:33000 scale ecology vegetation map (reduced to 1:99000 for publication in the thesis), in which the units are delimited and described on the basis of landscape forming factors such as soil characteristics and geomorphology - in addition to vegetation.

SABI SAND WILDTUIN

The Sabi Sand Wildtuin (SSW), in the south-eastern Transvaal Lowveld (centre of the reserve at 25"50'S, 31"33'E) borders the Kruger National Park (KNP) on the south and east and Gazankulu on the north and west (Figure 1). The reserve has an inverted L-shape and is approximately 570 km^2 in extent, lying on either side of the Sand river near its confluence with the Sabi river (Figure 1). The reserve lies in an intermediate topographic position between the Lowveld plain and the foothills of the eastern Transvaal great escarpment.

The SSW is one of three very large privately-owned game reserves

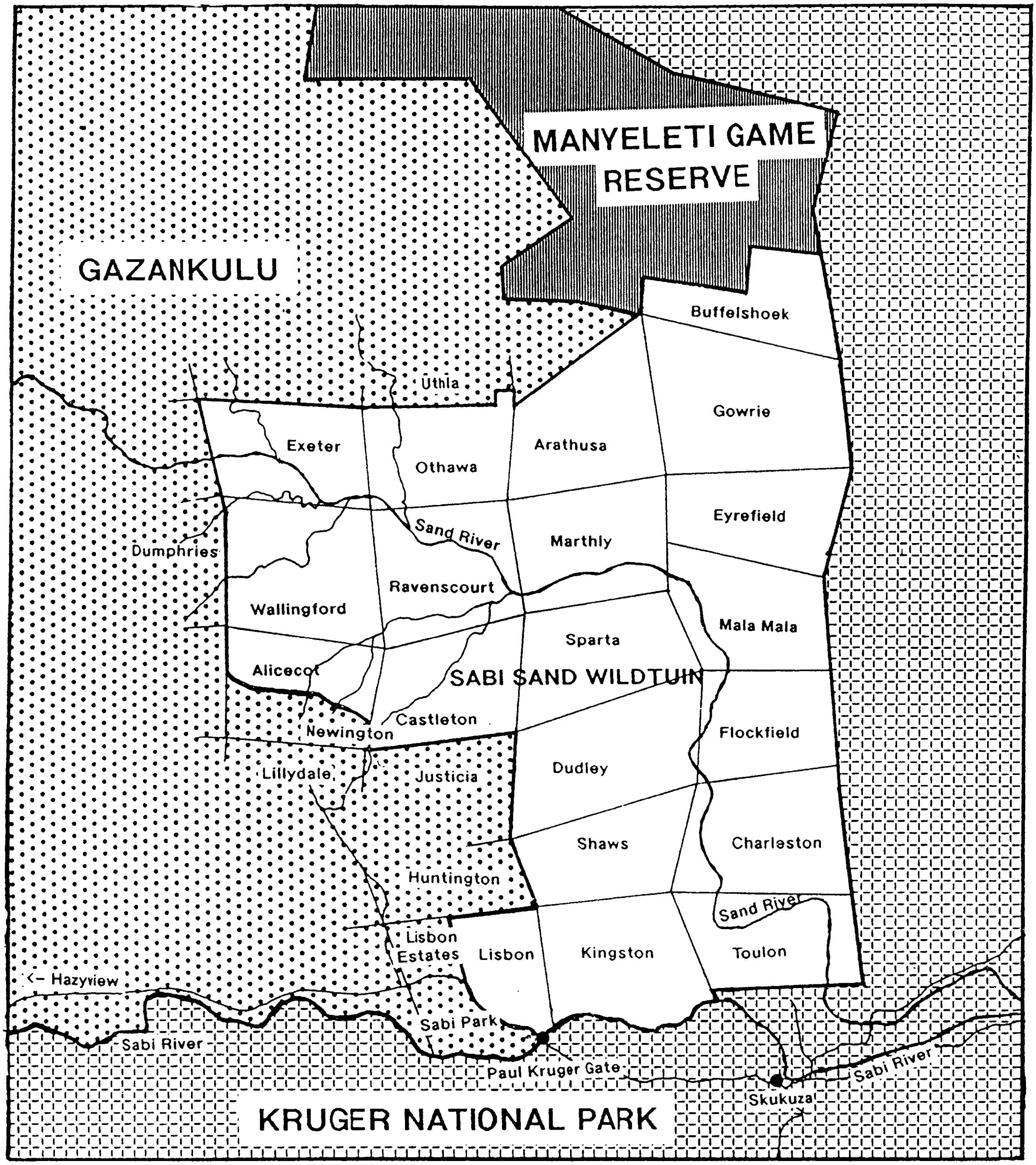


Figure 1. Map to show the location of the SSW in relation to the KNP, Manyeleti Game Reserve and Gazankulu, also shows position of the Sabie and Sand rivers.

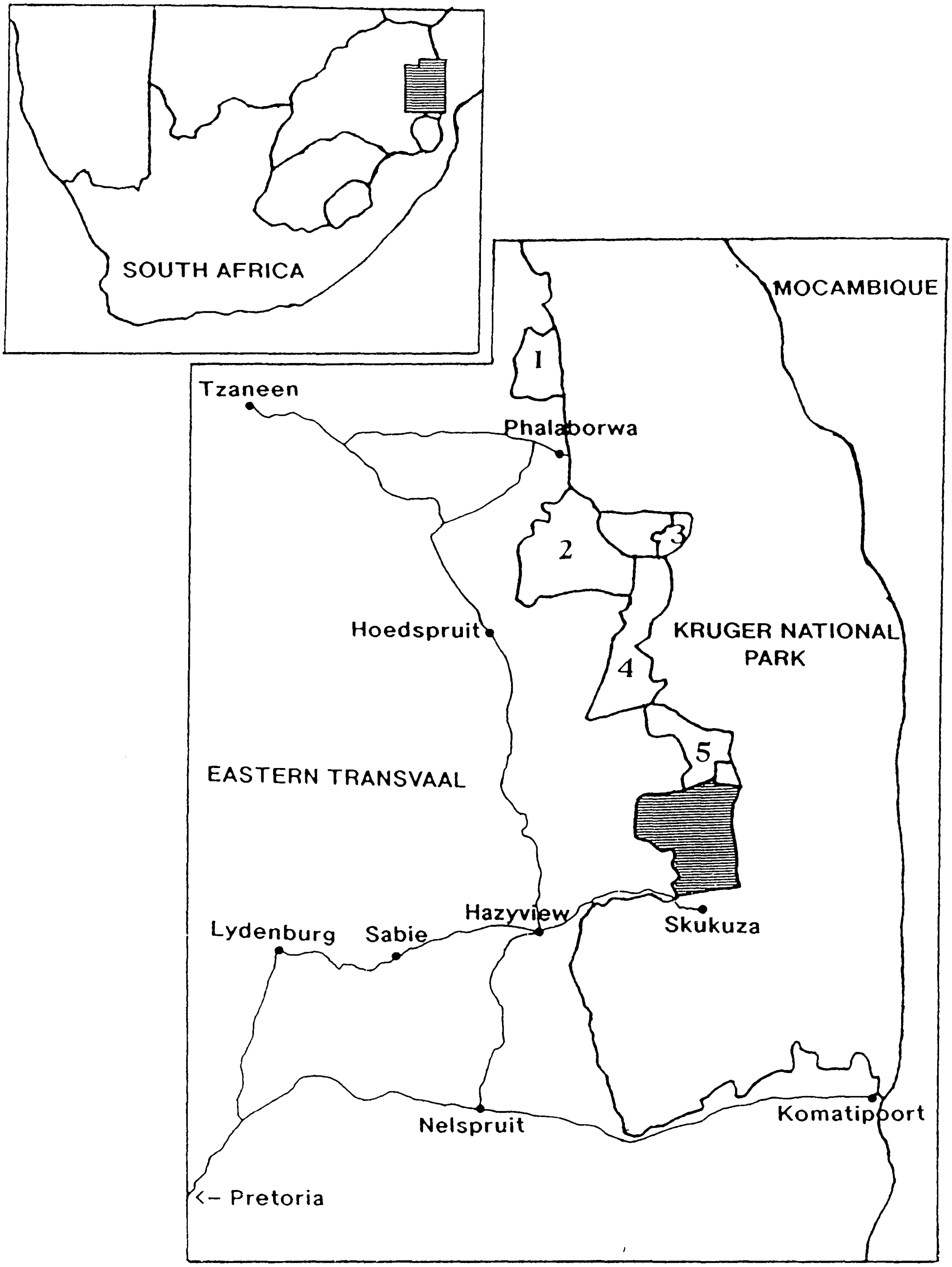


Figure 2. Map to show the location of the SSW in relation to the eastern Transvaal and South Africa. The other major private game reserves adjacent to the KNP are: 1) Letaba Ranch, 2) Klaserie, 3) Umbabat, Timbavati and 5) Manyeleti.

in the eastern Transvaal (the others being Klaserie and Timbavati). These three reserves together with the Manyleti and Shlaralumi game reserves form a continuous band from the Olifants to the Sabi rivers in the north and south respectively, forming a barrier between the KNP on the east and the private land and tribal homelands on the west (Figure 2).

HISTORICAL BACKGROUND

The Sabi Game Reserve was proclaimed in 1898 and in 1904 the entire area between the Sabie river in the south and the Olifants river in the north, bounded by the Lebombo and Drakensburg mountain ranges on the east and west respectively, was added to the Sabi Game Reserve (the predecessor of the current KNP). Thus for the first time the area today known as the SSW enjoyed protection as part of the Sabie Game Reserve.

Cattle ranching in the "Toulon Block" (which included the majority of the farms [holdings] at present part of the SSW) commenced in 1922. With the advent of cattle ranching official control over the area was terminated in 1923. Cattle ranching was to continue until 1934 at which stage the Transvaal Consolidated Land and Exploration Company, known as the TCL, sold their holdings. The farms today comprising the SSW were purchased by people like Wac Cambell, J. Arthur and G. Armstrong, who were interested in nature conservation and hunting. The owners at that time, included a number of farms in a nature conservation scheme known as the "Sabie Private Game Reserve" under the protection of the Transvaal Land Owners Association. Most farms comprising the present SSW had been included in the scheme by 1948 (Graupner 1971, Rattray 1986).

Today the SSW consists of a group of 19 unfenced privately owned farms operated as a conservation unit, being surrounded by a perimeter fence. Agricultural practices such as crop and/or stock farming are prohibited. Tourism on an increasingly large, but well organized scale, and hunting (on a limited scale) are pursued and the prime objective of many landowners remains to restore and maintain the SSW as nature reserve with a balanced ecosystem. As a result, the entire reserve is at present managed as an ecological unit by an elected management committee, assisted in their efforts by a game warden and several rangers.

CLIMATE

The SSW experiences a unimodal subtropical savanna climate with a single rainy season. The reserve lies in the summer rainfall region of southern Africa with dry winters. Perhaps it is more accurate to divide the climate of the SSW into three main seasons; a moist hot summer from October to March inclusive, a dry cooler winter from April to July and a dry pre-summer from August to September (often extending into October) (Figure 3). Mid-summer dry spells or droughts frequently interrupt the rain sequence and the dry season is of seven months duration in the longterm.

The precipitation profile with relief across the eastern Transvaal great escarpment and Lowveld in the Sabie-Sand drainage basin is shown in Figure 4. Rainfall occurs mainly in summer, with the reserve being situated between the 700 mm isohyet in the south and the 550 mm isohyet in the north, close to the transition between arid and moist savanna biomes (Huntley 1982).

The reserve thus falls in the more moist end of the Arid Savanna Biome, or in an intermediate mesic moisture regime. Longterm moist-arid sequences exemplified by a 64-year record from Skukuza are shown in Figure 5. The longest arid period in this record was of fourteen years duration between 1943 and 1958. After three above average rainfall years another arid sequence of nine years followed until 1970 (Figure 5).

Mean monthly maxima did not fall below 28,5 °C in summer nor below 18,9 °C in winter, while mean monthly minima did not fall below 21,0 °C in summer nor 6,9 °C in winter. Maximum temperature extremes in the Sabie river valley reached 41,5 °C at Ulusaba Game Lodge and 39,5 °C at Newington Gate. Minimum recorded temperatures include - 1 °C in the Sabie river valley and 1,5 °C at Inyati Game Lodge. There was little difference between the maximum temperatures of hill top and valley floor locations. Minimum temperatures, however, were consistently lower in the depressions, particularly in winter when the difference reached 8 °C. This was due to temperature inversions at night causing cold air to flow into valleys and depressions. Classified as a moderate frost area (-5 °C to 0 °C) some frost occurs in the valleys from June until early August. This is sufficient to reduce the nutrient value of the valley grasslands. The temperature range was smallest in December being 5,5 °C on average compared to the 22,9 °C in June at the time of least cloud cover (3.7% average).

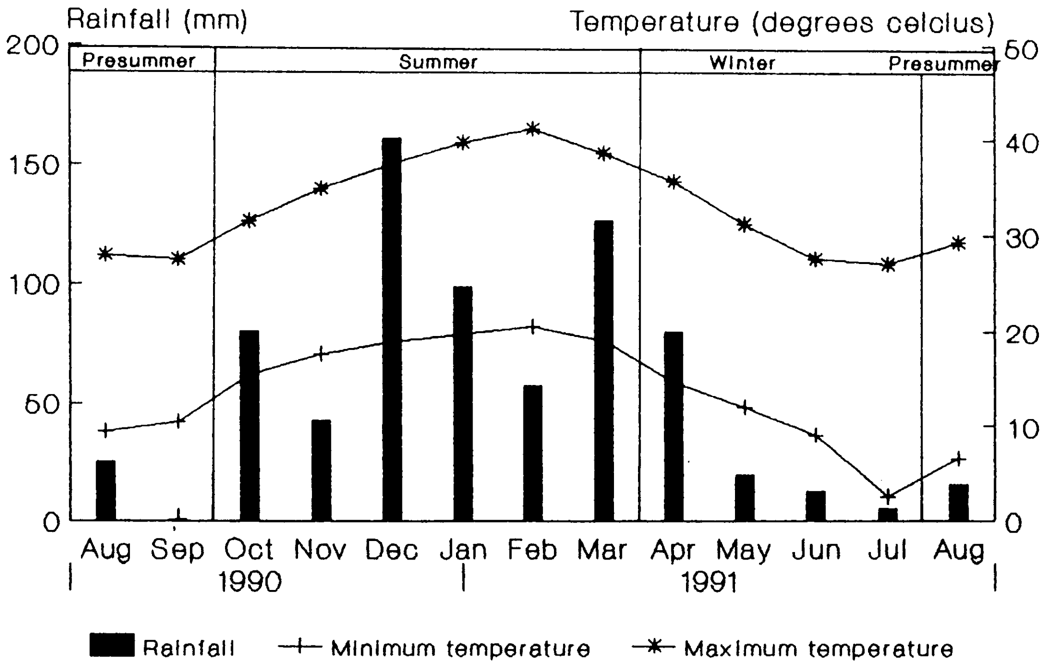


Figure 3. Monthly rainfall and mean maximum and minimum temperatures for the months July 1990 to August 1991, to illustate the three seasons.

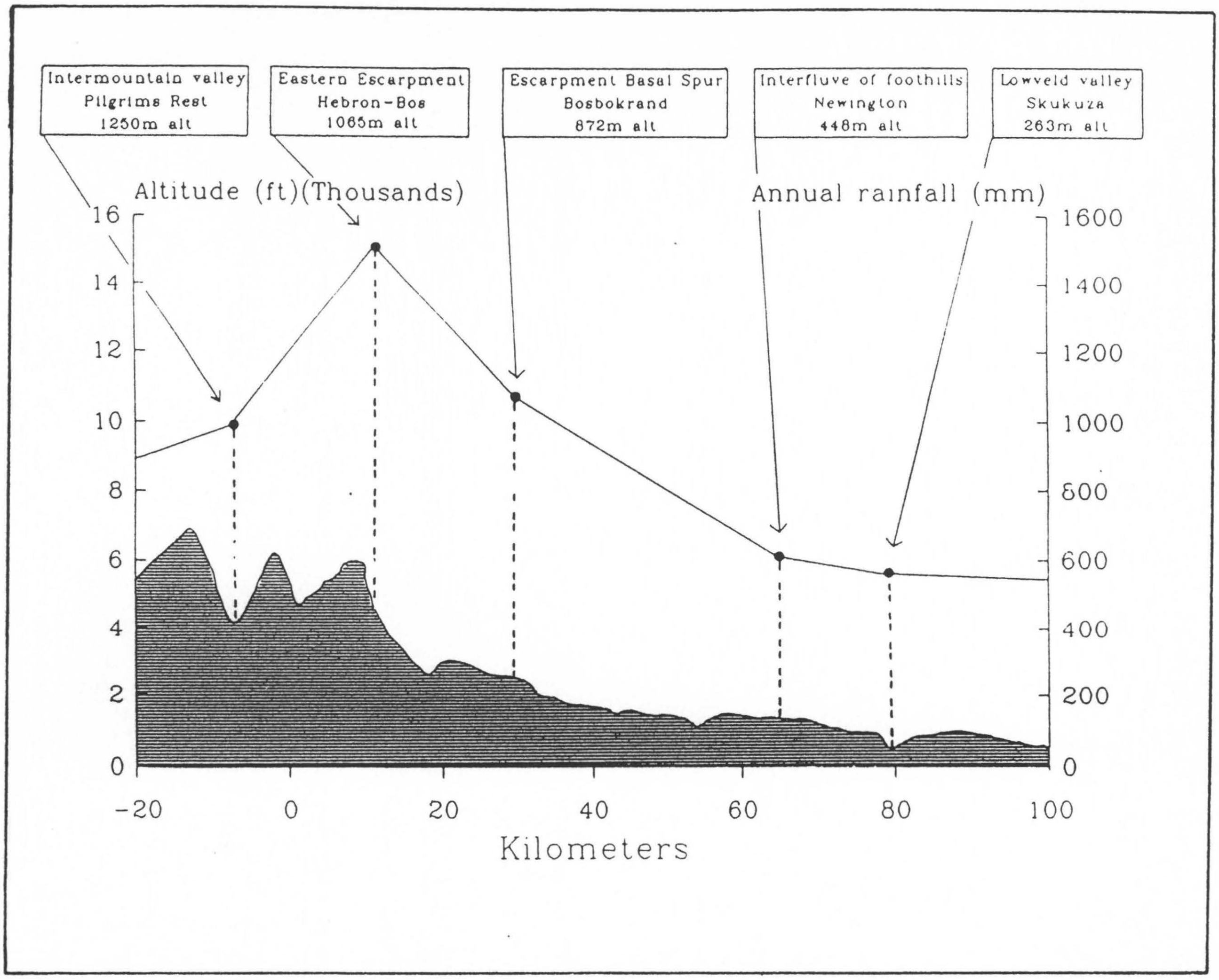


Figure 4. Close parallel of the rainfall across the eastern Transvaal Lowveld and great escarpment in the Sabie-Sand drainage basin.

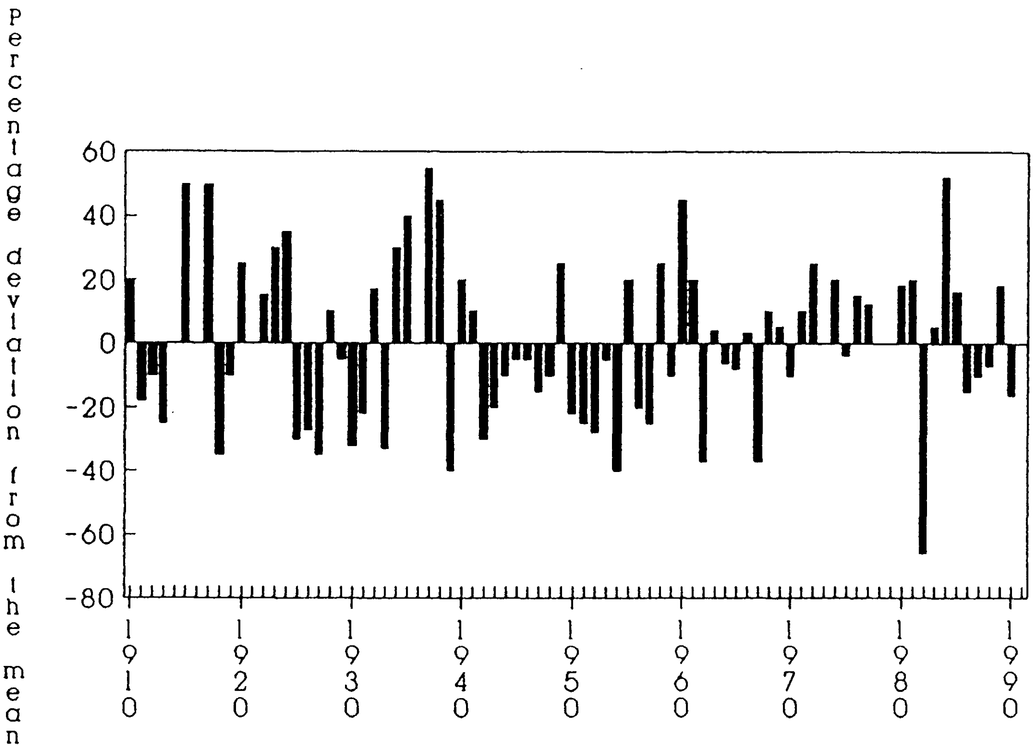


Figure 5. Longterm moist-arid sequences in the Transvaal Lowveld adjacent to the SSW as recorded at Skukuza since 1910, with a mean annual rainfall of 577 mm/year.

PHYSIOGRAPHY

TOPOGRAPHY, DRAINAGE AND WATER

The SSW lies in an intermediate topographic position between the Lowveld plain and the foothills of the eastern Transvaal great escarpment. The landscape is composed of moderately dissected, gently rounded hill country which rises 100 - 200 m above the floor of the Sand river valley. The reserve has its highest hill at Newington (484 m above sea level [a.s.l.]) and the highest point at Wallingford (Ryk) Koppies (548 m a.s.l.). The Sand river enters the SSW at 404 m a.s.l. and leaves 54 km further down at 274 m a.s.l., a difference in latitude of only 130 m and a gradient of 1:442. Topographic features are shown in Figures 6a - 6e.

The Sand river forms the main perennial water base line running across the centre of the reserve. During the wet season surface water occurs in numerous pans, drainage lines and streams. Most of the tributaries within the reserve are seasonal with pools persisting well into the dry season as on the Mobeni, Tsogwane, Mlowati, Matshapiri, Mshabane' and Usutu rivers.

A few permanent springs occur, the most important of which rises from the dolerite sill on the farm Dudley. Some of the seeplines ooze water perennially in median to high rainfall years, but are dry when midsummer droughts prevail in years with less than mean annual rainfall. Doleritic waters are generally brackish and those from seeplines acidic.

In order to supplement the sources of natural water available, especially during the dry months, a large number of catchment dams, boreholes and man-made waterholes have been provided. Most of these have permanent water in median to high rainfall years while the rain filled dams become dry in years with less than mean annual rainfall. Water provision in the SSW is shown in Figure 7. In high rainfall years 72%

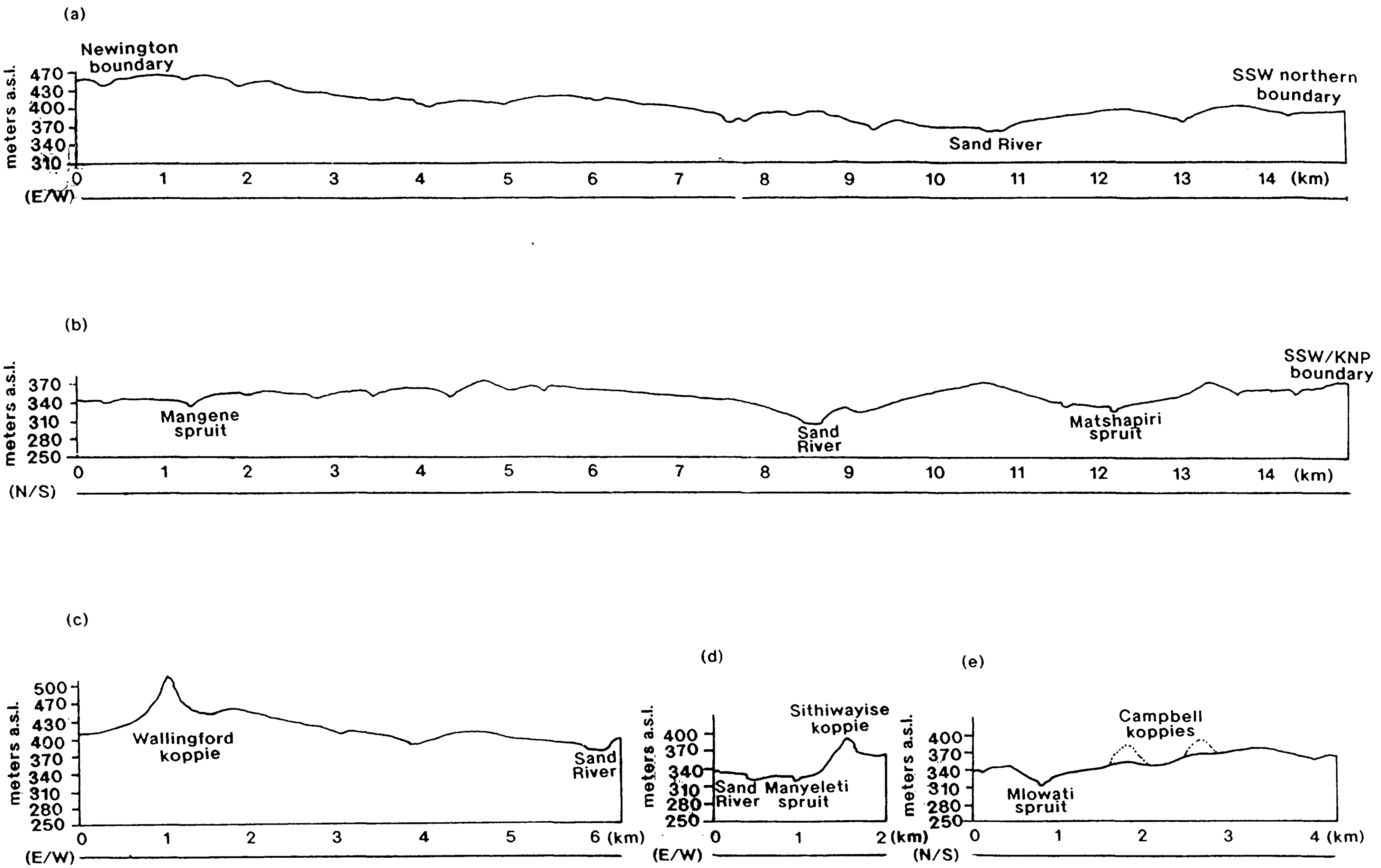


Figure 6. Topographic profile diagrams of different sections of the SSW along grid lines: a) 390, ± 31°25'E; b) 550, ± 24°49'S; c) 333, ± 31°21'E; d) 513, ± 31°32'E and e) 580, ± 24°47'S.

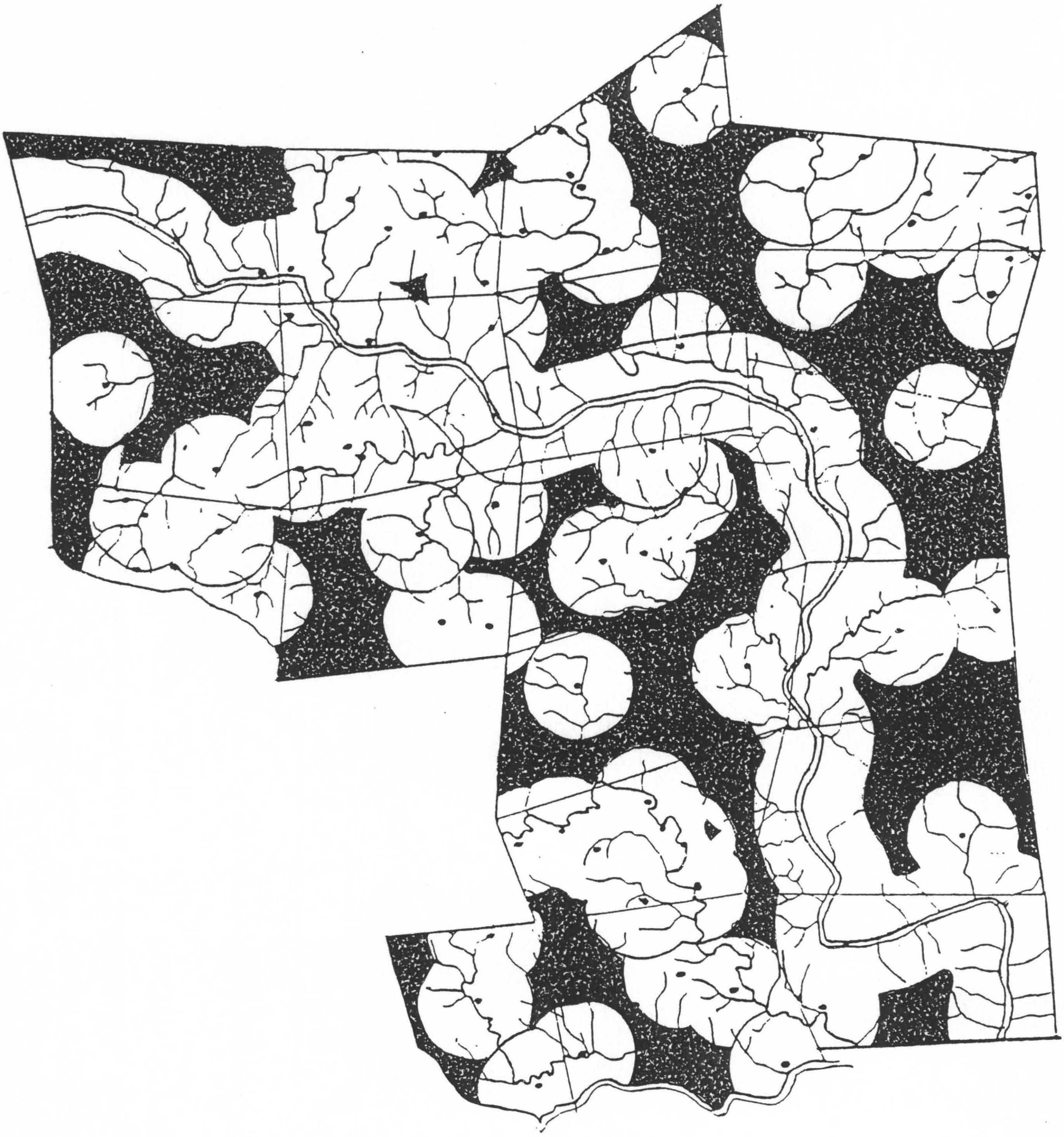


Figure 7. Drainage and water provision in the SSW. Drinking water is available to game within a radius of 1.5 km from a water point. Shading refers to the reliability of water points late in the dry season.

of the reserve is supplied with water during the dry season, and this decreases to 55% in low rainfall years.

GEOLOGY, SOILS AND THE LANDSCAPE CATENA

The geology and soils have been described by Tinley (1979). The major part of the country is developed on the extensive granite-gneiss system which is an acid intrusive volcanic rock (Bristow & Venter 1986). This generally granalitic system is dissected by dolerite basic volcanic intrusions (the Timbavati Gabbro) forming a grid of dykes and a large sill in the west central part of the reserve (Walraven 1983). Many of the doleritic dykes underlie granite topped inselbergs (koppies). The influence of the dolerite varies, resulting in three major basic combinations, homogeneous granite with very little or no doleritic influence, granite with rocky outcrops with medium to strong doleritic influence and dolerite dykes with wide belts of surface dolerite rock.

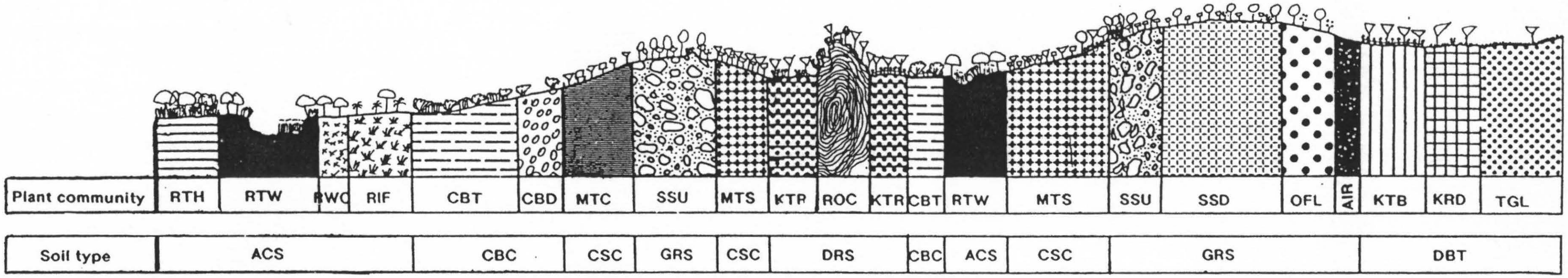
The present SSW landscape has been derived from a gently undulating plains land of sand convexities with intervening flat drainage lines, known as dambos in south central Africa. In their incision and headward erosion, stripping away the dambos, the rivers and dongas have exposed the contact between the deep red sand capping the hills and the underlying weathering front (saprolitic zone) of the granite along the contours. The granite saprolite is composed of rotten rock fragments in a matrix of maldrained saline sandy clay. The free draining red sand which overlies the maldrained subsoil absorbs part of the seasons rainfall resulting in lateral drainage. This ground water comes to the surface on the slopes of the hills along the contour where the subsoil surfaces, thus creating an extensive network of contour seeplines.

The seepline is composed of two quite distinct soils. An upper zone of acid white leached sands and a lower zone of base saturated grey-brown clays. Both soils are seasonally waterlogged in the rainy season so that the seepline zone is typically an open grass band devoid of trees and shrubs in undisturbed situations.

Lower down the slopes towards the stream gullies the soils are very variable, according to the amount of dolerite influence. These are either a shallow continuation of calc-brack clays or dark skeletal, sandy, often stony, extensively drained soils. In the valleys there are a variety of sedimentary soils derived from colluvium and alluvium. These are sandy, silty or black clays.

Turf soils derived from weathered dolerite are of two types. Red turf (clays) have some through drainage and are generally leached to partly leached. The other is a black base saturated clay.

This sequence of hillcrest sand, composite seepline soils, clayey to skeletal slopes and bottom land alluvia is repeated regularly across the valleys and hills where particular soils and associated floral complexes form a connected series referred to as a catena. This catena sequence is shown diagrammatically in Figure 8.



GRASS COMMUNITIES

RIF	Riverine floodplain
TGL	Turf grassland
OFL	Old fields sand savanna
AIR	Airstips

SAVANNA COMMUNITIES

SSU	Sand savanna
SSD	Sand savanna – cleared
MTS	Mixed tree savanna
MTC	Mixed tree savanna – cleared
KTB	Knobthorn black turf savanna
KTR	Knobthorn red turf savanna
KRD	Knobthorn r.t. – cleared

THICKET COMMUNITIES

RTW	Riverine and tributary woodland
RWC	Riverine woodland – cleared
RTH	Riverine thicket woodland
ROC	Rock outcrop
CBT	Euclea thicket mosaic
CBD	Euclea thicket – cleared

SOIL TYPES

ACS	Alluvial silt, black clay or sand
CBC	Calc–brack clay
CSC	Clayey skeletal, colluvial
DBT	Doleritic black turf
DRS	Doleritic red sands
GRS	Granalitic red sands

KEY TO SYMBOLS

Y	Small Acacia species
⌒	Thickets
☂	Riverine (Ficus, Scothia, Diopyros)
ııı	Reedbeds
♡	Euclea divinorum
⫶	Pterocarpus rotundifolius
▽	Acacia nigrescens
♀	Sclerocarya caffra
Ψ	Euphorbia
⚲	Combretum species

Figure 8. Landscape catena profile diagram across the SSW, showing the major soil types and associated habitat types.

THE LANDSCAPE

METHODS

The vegetation associated with the types of terrain have not been described in detail and it was, therefore, necessary to do this. Panchromatic black-and-white aerial photographs of the reserve (scale 1:50000, enlarged to an approximate scale 1:16700) made in 1986 provided the starting point for the survey. Using the aerial photographs apparent homogeneous textural units were stratified. It was presumed that these units were relatively homogeneous vegetation units (HVU), with various species in common, but with their arrangement and distribution on at least a micro-scale being more or less random. In order to identify and validate these HVU's it was necessary to sample the study area systematically. The field survey was carried out between August and October 1990. Most grass, shrub and tree species where identified in the field, some samples being taken to the herbarium at Skukuza for subsequent identification.

In order to prevent stratifying at too fine a scale, it was decided to restrict the HVU's to a minimum size of 4400 m^2, which equated to 12 x 12 mm grid squares at 1:16700 scale and 4 x 4 mm grid squares at 1:50000. A 4 x 4 mm grid was generated and overlaid on the 1:50000 HVU chart. Random numbers were generated to ensure that a minimum of four random samples were conducted per HVU.

This sampling technique follows the guidelines set out by Westfall & Panagos (1988) and Westfall (*pers. comm.* 199O), the sample sight being an estimated circular shape with a radius of 50 m. In the random generation of sampling sites it was essential to ensure that sampling sites were more than 150 m apart to ensure a 50 m radius sampling area and 50 m neutral zone.

DATA COLLECTION

When recording the species composition in a sample site one places each plant species to be sampled into distinct classes (Table 1). One then records the frequency with which each plant species occurs on a variable-sized belt transect. In order to determine the length of the transect one estimates the mean canopy diameter for the species and records which class interval it fits into (see Table 2). To determine the width of the transect one multiplies the mean canopy diameter by a factor of 0,8. The transect is then walked and the frequency with which the plant species occurs within the bounds of the transect is recorded.

Subsequent analysis reveals frequency of occurrence classes which can be used to determine indicator species for the various habitat types. These estimates combined with soil type and physiographic characteristics were used to produce the landscape vegetation map (Figure 9) and the landscape catena profile diagram (Figure 8). The percentage km^2 contributions of the various vegetation types were determined by using an image analyser (Dr. H.M. Dott *pers. comm.*).

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Table 1. Vegetation classes used for the survey.

Name	Symbol	Vegetation characteristic
Tree	T	single stem >2 m
		multi stem >5 m
Shrub	S	single stem <2 m
		multi stem <5 m
Dwarf shrub	D	woody <1 m
Grass	G	monocotyledon
Forb	F	includes sedges, forbs, etc.

Table 2. Class intervals of crown diameters according to the Fibonacci sequence for determining standard transect lengths.

Crown diameter class interval (m)	Transect length (m)
0.001-0.01	0.15
0.011-0.02	0.45
0.021-0.03	0.75
0.031-0.05	1.20
0.051-0.08	1.95
0.081-0.13	3.15
0.131-0.21	5.10
0.211-0.34	8.25
0.341-0.55	13.35
0.551-0.89	21.60
0.891-1.44	34.95
1.441-2.33	56.55
2.331-3.77	91.50
3.771-6.10	148.05
6.101-9.87	239.55

RESULTS AND DISCUSSION

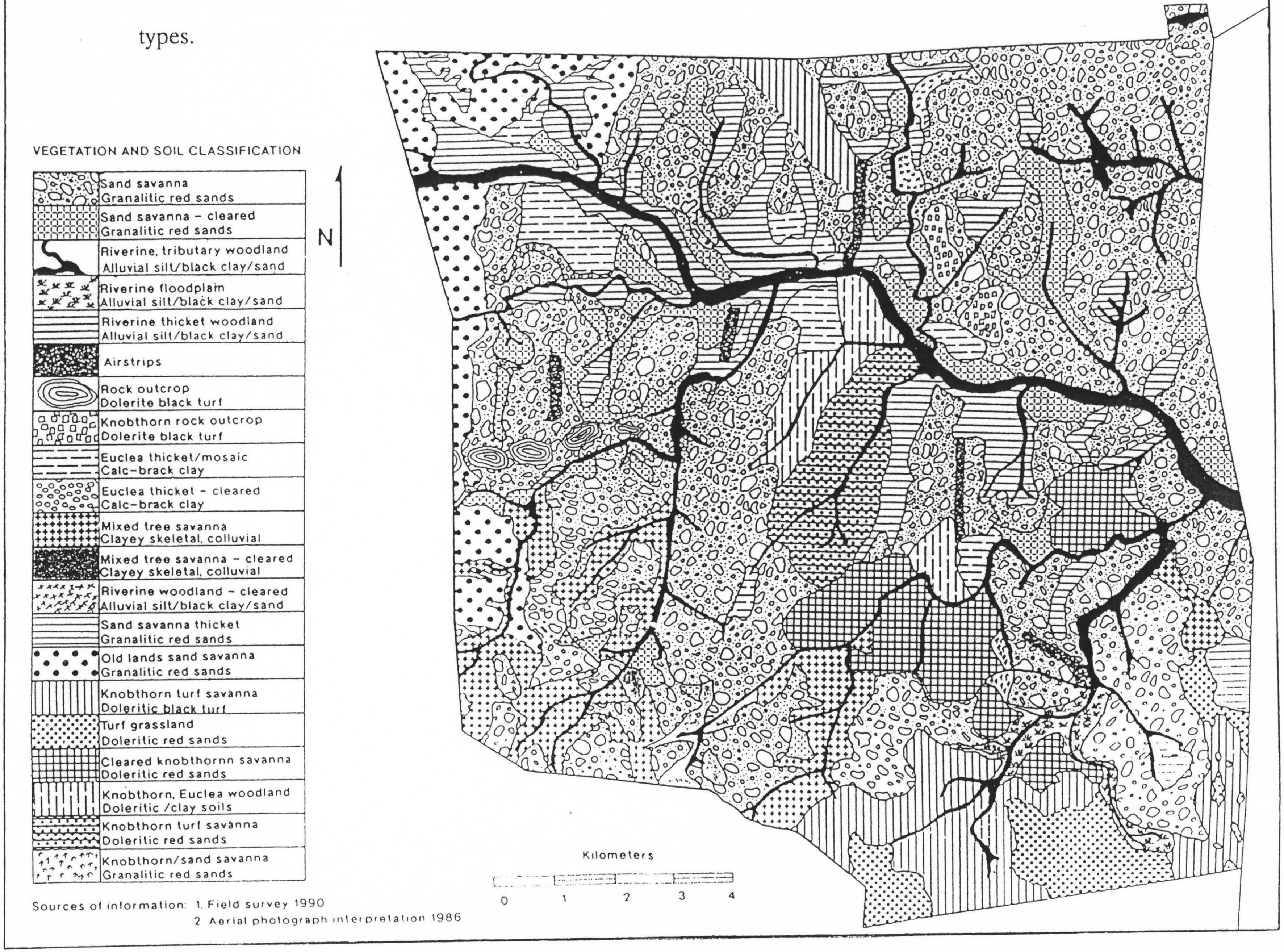
In a general context the vegetation of the SSW as part of the south eastern Lowveld is classified by Acocks (1975) as Lowveld (veldtype No. 10). As was found in the vegetation survey, the vegetation can further be divided into a number of plant communities on a local scale, based primarily on soil type and drainage characteristics. The main vegetation type divisions in the study within the SSW are summarized in Table 3.

The main plant community relationships with various substrates was resurveyed (after Tinley 1979), in the study area and some are illustrated by means of profile diagrams from examples in the field (Figures 10). These diagrams show the following features: appearance, structure, composition and cover. The various vegetation types are mapped on Figure 9. Considerable variation both in the structure and species composition occur within most plant communities, owing to the level of disturbance caused by overgrazing, bush encroachment and bush clearing.

The riverine areas are relatively small (RIF 0.85% + RTW 8.61% = 9.46%) as far as the area covered is concerned and confined to the Sand river and its major tributaries. These areas are important as they are the ultimate water and food base in extreme drought periods and remain green longest in the dry season. They are of particular importance to browsers and thicket preferring species because they and the riverine thicket woodland (RTH 9.4%) are the least deciduous of all plant communities.

A stable riverine and tributary woodland (RTW) system consists of tall trees such as sycamore fig *Ficus sycamorus*, jackal berry *Diospyros mespiliformes*, water berry *Syzygium cordatum*, tree fuschia *Schotia brachypetala*, sausage tree *Kigelia africana*, leadwood *Combretum imberbe*, matumi *Breonadia salicina* and brack thorn *Acacia robusta*.

Figure 9. Vegetation map of the study area in the SSW, showing the major habitat types.



Sources of information: 1. Field survey 1990
2. Aerial photograph interpretation 1986

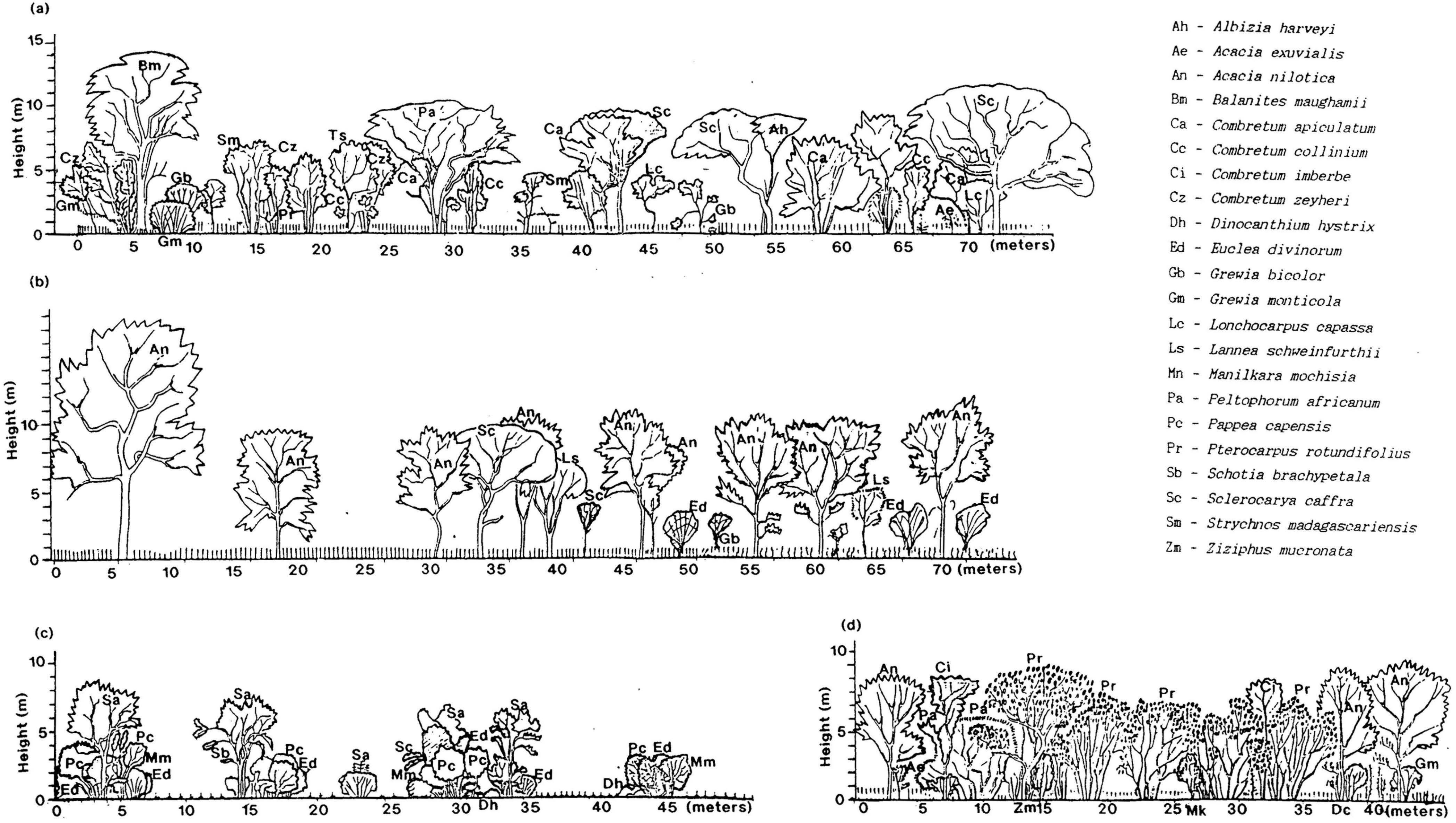


Figure 10. Habitat profile diagrams along four meter wide belt transects depicting typical growth form of some of the important plant communities in the SSW (redrawn from Tinley 1979): a) Marula-*Combretum* sand savanna, b) Knobthorn turf savanna, c) *Euclea* thicket and d) *Pterocarpus rotundifolius* encroachment of sandveld.

Table 3. Area in km² and percentage contribution of the various habitat types in the study area within the SSW.

Habitat	km²	percentage
Grass communities:		
1. Riverine floodplain (RIF)	1,43	0,85%
2. Turf grassland (TGL)	4,68	2,76%
3. Old lands sand savanna (OFL)	8,24	4,87%
4. Airstrips (AIR)	1,08	0,64%
Savanna communities:		
5. Sand savanna (SSU)	71,23	42,15%
6. Sand savanna - cleared (SSD)	10,14	5,99%
7. Mixed tree savanna (MTS)	7,38	4,37%
8. Mixed tree savanna - cleared (MTS)	2,15	1,27%
9. Knobthorn savanna (black turf) (KTB)	10,43	6,17%
10. Knobthorn savanna (red turf) (KTR)	7,47	4,42%
11. Knobthorn sav. (red turf) - cleared (KTD)	7,21	4,27%
Thicket and forest communities:		
12. Riverine and tributary woodland (RTW)	14,55	8,61%
13. Riverine woodland - cleared (RWC)	0,56	0,33%
14. Riverine thicket woodland (RTH)	15,89	9,40%
15. Rock outcrop (ROC)	1,49	0,88%
16. *Euclea* thicket mosaic (CBT)	4,89	2,89%
17. *Euclea* thicket - cleared (CBD)	0,69	0,41%
TOTAL	169,01	100,00%

The shrubs are red spike thorn *Maytenus senegalensis*, flame creeper *Combretum microphyllum*, wild date palm *Phoenix reclinata*, mlala palm *Hyphaene natalensis*, hairy lavender fever berry *Croton gratissimus* and *Albizia* species. The main grasses are *Panicum maximum*, *Cenchrus ciliaris*, *Eragrostis* spp, *Urochloa mossambicencis* and *Cynodon dactylon* while *Phragmites australis* is of importance in the wet bases of the river.

In overgrazed and encroaching areas scented thorn *Acacia nilotica*, red spike-thorn, russet bushwillow *Combretum hereronse* and grasses like *Setaria megaphylla*, *Digitaria eriantha*, *Aristida* spp and *Pogonathria squarrosa* become prominent.

In a riverine floodplain (RIF) many of the large trees mentioned above are absent and the relatively flat floodplain area is dominated by wild date and mlala palms, there is reduced cover by shrubs and a similar grass community to that mentioned in the above riverine areas.

The riverine thicket woodland (RTH) community borders on the RTW system, especially along the Sand and Madji Mabhiri river systems extends some distance into the veld away from, the RTW system. The system consists of tall trees such as jackal berry, tree fuschia, black monkey thorn *Acacia burkei*, Natal mahogany *Tricheila emitica*, apple-leaf *Lonchocarpus capassa*, buffalo thorn *Ziziphus mucronata*, tamboti *Spirostachys africana*, green thorn *Balanites maughami*, leadwood, russet bushwillow and sausage tree. Shrubs include red spike thorn, common spike thorn *Maytenus heterophylla*, Pride-of-De Kaap *Bauhinia galpini*, potato bush *Phyllanthus reticulatus*, porcupine bush *Dinocanthium hystrix* and dwarf boer-bean *Schotia capitata*. The main grasses are *P. maximum*, *Eragrostis* spp, *U. mossambicencis* and *C. dactylon*.

The riverine woodland - cleared (RWC) is a very small system (0,33%) and comprised purely of leadwood trees with a similar grass community to that described above, including *P. squarrosa*, *U. mossambicencis* and *Heteropogon contortous*. This is a totally unnatural system which arose through clearing the RTH.

The turf grassland (TGL 2,76%) is an open woodland scattered with trees like knobthorn *A. nigrescens*, marula *Sclerocarya caffra*, tree wistaria *Bolusanthus speciosus* and apple-leaf. This is a *Themeda triandra* climax grassland when undamaged, but when overgrazing occurs it is replaced by unpalatable, wiry grasses, especially *Bothriochloa insculpta*, *Cymbopogon excavatus*, *C. plurinodis*, *Enteropogon monostachys* and *E. plana*. Stunted trees encroach, the more important being round-leaved kiaat *Pterocarpus rotundifolius*, sickle bush *Dichrostachys cinerea*, *Grewia* spp, russet bushwillow and red spike thorn.

The undisturbed sand savanna (SSU) is the largest vegetation type (42,15%) in the study area. Tree species are mainly red bush willow *C. apiculatum*, marula, large-fruited bushwillow *C. zeyheri*, weeping bushwillow *C. collinium*, zebra wood *Dalbergia melanoxylon*, wild pear *Dombeya rotundifolia*, Transvaal teak *Pterocarpus angolensis*, silver cluster-leaf *Terminalia sericea*, false currant resin *Ozoroa insignis*, buffalo thorn and green thorn; with *P. maximum*, *P. coloratum*, *T. triandra*, *Digitaria* spp, *Eragrotis* spp, *Elionurus muticus* and *H. contortous* as the common grasses. Common shrubs include common spike thorn, white raisin Grewia bicolour, silver raisin *G. monticola* and sourplum *Ximenia caffra*.

Damaged sandveld consists of very dense stands of smaller large-fruited bushwillow, round-leafed kiaat, black monkey orange *Strychnos madagascarensis*, sickle bush, and flacky thorn *Acacia exuvialis* becoming prominent below the main stand of red bush willow and marula. Grass cover reverts to annuals such as *Mellinis repens*, *Tragus berteronianus*, *Perotis patens*, *P. squarrosa*, *A. congesta* and *Eragrostis superba*.

Sandveld that has been cleared (SSD 5,99%) is characterized by large trees such as marula, zebra wood, wild pear and green thorn. Few shrubs are left and the grass community is similar to that of an SSU, but many of the annuals listed above are present, with *P. maximum* being stunted or absent. Stable seeplines exist on the slopes of the sandveld ridges and if undamaged consist predominantly of silver cluster-leaf. Typical grasses are *E. gummiflua*, *P. maximum* and *T. triandra*. The silver cluster-leaf is a very important indicator of damaged seeplines. Large-fruited bushwillow, red thorn *A. gerrardii*, common false thorn *Albizia harveyi* and sickle bush are typical invaders together with indicator grass species such as *Hyperthelia dissoluta*, *Dactyloctenium aegyptium*, *Aristida meridionalis*, *Bracharia nigropedata*, *P. patens*, *E. plana*, *C. dactylon* and *P. squarrosa*.

Old lands savanna (OFL 4,87%) consists of areas that have been occupied by Shangaan people in the last one hundred years. Most of the large trees of this once undisturbed sand savanna have been chopped down and those that are left, namely marula, green monkey orange *Strychnos spinosa* and jackal berry, are all fruit producers and were thus of some use. The numbers of the common grasses of SSU have been reduced, and mainly annuals are present. The grasses include: *P. coloratum*, *T. triandra*, *H. contortous*, *M. repens*, *T. berteronianus*, *P. patens*, *P. squarrosa*, *A. congesta* and *E. superba*.

The mixed tree *Acacia-Combretum* slope savanna (MTS 4,37%) is associated with areas varying greatly depending on soil type and soil depth. It is fairly well wooded with good grass cover. In a stable state the main tree species are knobthorn, red bushwillow, leadwood, weeping bushwillow, marula, black monkey thorn, zebra wood, sickle bush *Grewia* spp (raisin bush) and weeping wattle *Peltophorum africanum*, with palatable grasses such as *P. maximum*, *P. coloratum*, *T. triandra* and *U. mosambicensis* predominating. When damaged tree species like flaky thorn, scented thorn, three hooked thorn and red thorn, round-leafed kiaat and *Combretum* spp form dense stands and thickets. Grasses including *B. insculpta*, *C. plurinodis*, *A. c. barbicolis*, *A. congesta*, *E. monostachys*, *E. superba* and *E. rigidor*.

In areas where the natural MTS has become encroached bush clearing has been conducted with marula, bushwillow and zebra wood trees being left. The cleared mixed tree savanna (MTD) is a relatively small area (1,27%) on the farm Alicecot, but has palatable grasses such as *P. maximum*, *P. coloratum*, *T. triandra* and *U. mosambicensis* predominating.

Knobthorn turf savanna's occur on two soil types, namely black turf soils and red turf soils. Both knobthorn black turf savanna (KTB 6,17%) and knobthorn red turf savanna (KTR 4,42%) in their stable states are typically knobthorn/*T. triandra* woodland with patches of white raisin bush. However, with overgrazing this grass climax becomes thickly encroached with *Acacia* spp, sickle bush and round-leafed kiaat while the grass substratum reverts to the typically wiry unpalatable species such as *Cymbopogon* spp, *B. insculpta*, *Aristida* spp, *Eragrostis* spp and *Sporobolus nitens*. In the study area especially, KTR has been encroached by the scented thorn and there are a fairly high number of marula and magic guarri *Euclea divinorum* trees. Much of the KTR has been cleared and the cleared knobthorn red turf savanna (KRD 4,27%) is now predominantly knobthorn dominated, however, in some areas the unpalatable grasses mentioned above predominate. Some areas of KRD have shown tremendous recolonization by *T. triandra*.

Rock outcrops (ROC) constitute a very small percentage of the study area (0,88%). Large trees such as marula, knobthorn, red bushwillow, white seringa *Kirkia acuminata*, common cabbage tree *Cussonia spicata* and candelabra tree *Euphorbia cooperi* predominate and in the sheltered conditions *P. maximum* thrives. Due to the steepness of the terrain the ROC habitat is not heavily selected for by large mammal species.

The *Euclea* calc-brack savanna mosaic and thickets (CBT 2,89%) are associated mainly with the lower slopes and drainage areas of the granalitic duplex soils. It is another important habitat providing browse into the driest time of the year and sweet grass conditions. When undamaged the vegetation consists of open grassland, bush clumps and savanna mosaics. The main tree species are magic guarri, jacket plum *Pappea capensis*, tree fuschia, tamboti, dwarf boer-bean, common spike thorn, Lowveld milkberry *Manilkara moschisia*, Transvaal saffron *Cassine transvaalensis*, and false marula *Lannea schweinfurthii* as bush clumps, often associated with termitaria, with spread out knobthorn, scented thorn, common false thorn and leadwood as bigger trees. The climax grass species are *T. triandra*, *P. maximum*, *U mosambicensis* and *Digitaria eriantha*.

This is one of the main plant communities suffering from, soil erosion, overgrazing and bush encroachment. The important encroaching species are magic guarri, scented thorn, red thorn, flaky thorn, caterpillar bush *Ormocarpum trichocarpum*, weeping wattle, zebra wood, russet bushwillow, worm-bark false thorn *Albizia anthelmintica* and Transvaal gardenia *volkensii*. Encroaching shrubs include sourplum, false spike-thorn *Putterlickia pyracantha*, porcupine bush and potato bush. The grass cover when overgrazed becomes dominated by grass species such as *A. c. barbicolis*, *Sporobolus nitens*, *E. superba* and *P. squarrosa*. Forbs also encroach when damage is excessive. A small percentage (CBD 0,41%) of CBT has been cleared to try and reestablish a natural veld type.

Airstrips (AIR) also constitute a very small surface area. Most are gravel strips with no grass cover, but some are covered by short grass such as *S. nitens*, *A. congesta* and *P. squarrosa*.

ASSESSMENT OF VELD CONDITION/SEASONAL BIOMASS CHANGE

INTRODUCTION

Veld condition refers to the condition of the vegetation in relation to some functional characteristic, normally sustained forage production and resistance of the veld to soil erosion (Trollope, Potgieter & Zambatis 1989). The technique used for estimating veld condition was developed by these authors, and was used for estimating veld condition in the various vegetation types determined by the survey.

METHODS

The first step in assessing veld condition is to sub-divide the survey area into homogeneous vegetation units (HVU). Assessment was made of the veld occurring within each HVU, based on species composition, at one or more sample sites. The key species in these samples were given forage and fuel indices which were used in the calculation of condition and trend. From the collection of key species data in the various habitats it was possible to determine objective estimates of the proportions of decreaser, increaser I and increaser II grass species. Decreaser grass species (DEC) are species which reduce in number when the veld is under or overutilized. Grass species that increase in number when the veld is underutilized are classified as increaser I grass species (INC I), and those that increase when the veld is overutilized as increaser II grass species (INC II) species. There were at least ten sample sites in each habitat type with 100 samples being taken at each sample site in the three seasons. Overall condition of the veld in the survey area was calculated using the proportional contribution of each HVU to the total area (Trollope *et. al.* 1989).

A measure of the seasonal availability of grasses was provided through the variations in dry matter yield. Biomass changes were monitored with the use of a disc pasture meter calibrated for the area (Trollope & Potgieter 1986). This instrument was developed by Bransby & Tainton (1977) for estimating grass fuel loads. The technique employs a central aluminium rod 180 cm long supporting a sleeve and an aluminium disc 45,8 cm in diameter, which slides freely along the rod. When operating the disc meter the operator allows the disc to slide down the rod. The disc stops at a certain height above the ground level which is determined by the density of grass tufts. The central rod, marked at 1 cm intervals, was held perpendicular to the ground surface while a sleeve with the attached disc was released onto the sward from a standard position levelling the upper end of the sleeve with the upper end of the rod. The setting height of the disc was then read off the rod from the position corresponding with the upper end of the sleeve.

One thousand readings were taken in each habitat in each of the three seasons. The average readings represented the total biomass of grasses, per habitats, per season, and were then converted to dry matter yields by using the following linear regression relationship which was developed for this region (Trollope 1983):

$$Y=-3019+2290\sqrt{X}$$

where Y=Forage biomass (kg/ha) and X=Mean disc height (cm).

RESULTS AND DISCUSSION

The results of the veld condition and available forage assessment are summarized in Table 4. Trends in biomass change over the seasons and estimates of veld condition in terms of forage potential, fuel potential and indicator grass species have become apparent from the analysis.

The undisturbed sand savanna (SSU) is the largest vegetation type (42,15%) in the study area, and is a medium to thickly wooded community with a relatively sparse grass cover. The mean available dry forage in the summer was 2845 kg/ha, but this was reduced to 1956 kg/ha by the presummer months. This closed woodland habitat was extensively used by wildebeest *Connochaetes taurinus*, zebra *Equus burchelli* (*pers. obs.*, Ben-Shahar 1991) and especially buffalo (*pers. obs.*), resulting in a large reduction in biomass. The mean forage and fuel scores range from 400 - 500 which is indicative of a high potential. On average there is a 46% proportion of DEC. These are highly palatable, and grazing pressure may be responsible for the high (49%) proportion of INC II.

The cleared sand savanna (SSD) areas (5,99%) were characterized by having forage (304) and fuel (395) scores that were indicative of a low potential. The forage score was significantly lower than that for SSU ($t = 3{,}68$; $p < 0{,}01$; df = 8), but there was no significant difference between the fuel scores. The reason for the low forage potential was the significantly higher proportion of INC II than in SSU ($t = 4{,}35$; $p < 0{,}01$; df = 8). Possible reasons for this include increased utilization of the palatable DEC by open grassland grazers subsequent to the bush clearing. Biomass estimates ranged from 2218 to 1764 kg/ha, with the mean summer estimate of 1976 kg/ha lower than the mean winter estimate of 2218 kg/ha, which was as a result of a management policy to cut the clearings in order to prevent the regrowth of herbaceous species.

The old lands sand savanna (OFL 4,87%) show no significant difference in terms of available dry matter biomass to that of SSU, there was also no significant difference in terms of the ratio of DEC, INC II and INC II ($t = 0{,}98$; $p > 0{,}05$; df = 8). Forage and fuel potentials were also both high. It seems as if the previous occupation of this land by Shangaan people and their cattle has not had a deleterious result in comparison with SSU. There is, however, still a relatively high (46%) proportion of INC II. Although this is an open savanna like that of SSD, no grass mowing is conducted and there is a higher proportion of woody species which may contribute to the significantly higher proportion of DEC ($t = 3{,}89$; $p < 0{,}01$; df = 8).

The mixed tree savanna (MTS 4,37%) habitat was characterized by fairly good grass cover with high forage and fuel potentials. The biomass of available forage was high in summer (2750 kg/ha) and was reduced to mean value of 2105 kg/ha by the presummer months. There was no significant difference between the proportion of DEC and INC II ($t = 0{,}56$; $p > 0{,}05$; df = 8) (Table 4).

The cleared mixed tree savanna (MTD 1,27%) was also characterized by fairly good grass cover with medium forage and high fuel potentials. Although there was only a medium forage potential there was no significant difference between the biomass estimates over the three seasons ($t = 1{,}45$ summer, $t = 1{,}67$ winter, $t = 1{,}12$ presummer; $p > 0{,}05$; df = 8). There was, however, a significant difference between the proportion of DEC and INC II ($t = 3{,}40$, $p < 0{,}01$; df = 8). The reason for the lower DEC may be due to increased herbivore pressure in the more open savanna.

In comparing knobthorn black turf savanna (KTB) with knobthorn red turf savanna (KTR) it became apparent that there was no significant difference in terms of biomass over the three seasons ($t = 2{,}10$ summer, $t = 1{,}85$ winter, $t = 0{,}98$ presummer; $p > 0{,}05$; df = 8). Both KTB and KTR had high biomass's in summer which were reduced by 18% and 33% respectively by the presummer months. KTB had high forage and medium fuel potentials, while KTR had very high forage and high fuel potentials. In both habitat types the DEC was significantly higher than the INC II, with *T. triandra* and *P. maximum* predominating ($t = 4{,}67$ KTB, $t = 5{,}11$ KTR; $p < 0{,}01$; df = 8).

In the cleared knobthorn red turf savanna the *T. triandra* climax grasslands have recovered, the habitat thus had high forage and very high fuel potentials. The ratio of DEC to INC II was almost the same as that of KTR (Table 4). The biomass estimates and seasonal reduction were also similar to KTR (Table 4).

The riverine and tributary woodlands (RTW) were characterized by very high forage and fuel potentials. The ratio of DEC to INC's was high with very high biomass, which ranged from 4530 kg/ha in summer to 3547 kg/ha in the presummer months (Table 4). In contrast the riverine thicket woodland was overutilized with only medium forage and fuel potentials, low RED to INC II ratio and constantly low biomass (1945 - 1856 kg/ha) over the seasons. High grazing pressure by impala *Aepyceros melampus*, waterbuck *Kobus ellipsiprymnus*, and hippo *Hippopotamus amphibius* may be responsible.

In most instances the *Euclea* calc-brack mosaic and thickets (CBT) were overutilized, resulting in bush encroachment and short unpalatable grasses. The mean available dry matter biomass ranged from 917 kg/ha in the summer to 178 kg/ha in the winter. These areas were extensively utilized by impala, wildebeest and warthog *Phacochoerus aethiopicus*. The ratio of DEC to INC II was very low, with very few palatable grass species. This area was characterized by very low forage and low fuel potentials, and it would require much less pressure by herbivores and clearing of thickets before this veld could recover (Table 4).

In a few (0,41%) areas the CBT has been partially cleared (CBD), resulting in significant increases in available forage (t = 3,38 summer, t = 3,98 winter, t = 4,23 presummer; p < 0,01; df = 8). The ratio of DEC to INC II has also shown some improvement, the forage potential is significantly higher than that of CBT, but the fuel potentials remain similar (t = 3,81; p < 0,01; df = 8) (Table 4). It is conceivable that the reduction in cover through clearing has led to fewer herbivores in this habitat and, therefore, to slight improvement in veld condition.

Table 4. Results of the veld condition and biomass assessment for the major habitats in the various seasons.

HABITAT TYPE	Forage		Fuel		Decr	Inc I	Inc II	BIOMASS (Kg/ha)		
	Score	Potential	Score	Potential	Mod	Under	Over	Sum.	Wint.	Pres.
SSU	495	high	440	high	46	4	49	2845	2390	1956
SSD	304	medium	392	medium	26	2	72	1976	2218	1764
OFL	387	medium	412	high	46	8	46	2673	2541	2006
MTS	423	high	468	high	45	7	48	2750	2344	2105
MTD	350	medium	458	high	38	5	57	2812	2400	2197
KTB	476	high	398	medium	62	-	38	2732	2387	2231
KTR	592	v.high	444	high	70	-	30	3229	2248	2156
KRD	425	high	518	v.high	69	-	31	3199	2754	2282
RTW	622	v.high	505	v.high	66	-	34	4530	3986	3547
RTH	351	medium	305	medium	32	3	65	1945	1909	1856
CBT	168	v.low	199	v.low	12	-	88	917	321	178
CBD	234	low	198	v.low	26	-	74	1159	1073	999

CHAPTER 3: PRELIMINARY AND BASIC RESEARCH PROCEDURES

INTRODUCTION

Field studies on movement, feeding and behaviour patterns of buffalo have been related to social and ecological conditions in an attempt to answer the key questions outlined previously. Certain of the research procedures are discussed in this chapter, while detailed descriptions are provided in the appropriate chapters.

LOCATING BUFFALO

Unlike most other ungulates, and indeed land dwelling mammal species found in South Africa, buffalo occur in large herds, utilize home ranges of an area greater than 150 km^2 and consequently a single herd could be anywhere within this area. For this reason the study was not confined to a small study area, as is usually the case with many studies of other ungulate species. Furthermore, the study was designed to study groups or herds of buffalo, the study area thus becoming the collective total of their specific home ranges.

Locating the few widely separated herds was a time consuming but essential exercise. It soon became apparent that to attempt to follow a number of herds was impractical, and thus data collection was concentrated on a herd of 230 buffalo in the northwest of the SSW. Observations, however, were made on the buffalo herd whose home range adjoined and overlapped that of the study herds home range, along its eastern boundary.

The daily research schedule started by driving out to the area where the buffalo were last observed. The vehicle was often used very effictively, due to the extensive network of roads in the study area, to check for the spoor of the herd crossing the road and to determine in which direction the herd had moved. If more tracks were not picked up along the road then the spoor was followed on foot until the herd was located. Tracing the herds' movements was more often done by "spooring" than by following the buffaloes closely. Radiotelemetry was not considered due to the relative ease with which the trained eye can follow the spoor of a herd of buffalo, the vast amount of information that could be assimilated while tracking the herds movements and the unsightliness and cost of radio collars. The average amount of time required to track down the herd during the study was 45 min by vehicle and 1 h 20 min when on foot. Information on the location of bachelor male and breeding herds of buffalo was also gained from guides working at the game lodges.

Observations made while tracking a herd of buffalo include direction of movement, habitat selection, watering points and an indication of activity (for example walking, resting, drinking, feeding patch). The combination of parameters observed while tracking buffalo allowed one to construct a time scale in order to enable the placing of deduced events in time.

OBSERVATION OF BUFFALO

Field observations were made from a Toyota four wheel drive vehicle and on foot. Contact with the herd could be maintained for indefinite periods when necessary, terrain conditions seldom impeded observation, unlike the work done by Mloszewski (1983) were he found that the buffalo usually traversed types of terrain that were not suitable for a vehicle. In particular, during periods of high rainfall observations were made on foot, especially when the buffalo were in turf soil areas, where vehicle tracks left in the mud damage the roads, and some terrain became impassable. Observations on general herd behaviour and movement were made from a suitable distance to avoid disturbance. While observations of individual behaviour were usually made from within the herd, provided it was on the move and grazing.

Mloszewski (1983) found that following a moving herd in a motorcar was usually unsatisfactory, as their behaviour was clearly affected by the presence of a moving vehicle. In the present study, the buffalo herds became habituated to the presence of vehicles, and although a vehicles presence would alert the animals in close proximity, it did not affect the activity of animals further away, or the direction in which the herd was moving. It can only be presumed that the buffalo that Mloszewski studied were not as exposed to vehicles or that they were regularly pursued by hunters.

RECORDING OF SPATIAL DISTRIBUTION DATA

One of the aims of this study was to investigate the spatial organization of the African buffalo in the SSW. This was only possible by pinpointing one's exact location on a map of the study area. Consequently, mapping, orientation and the accurate recording of spatial distribution data were of great importance.

Regular 1:50000 maps available from the Government Printers and black and white 1:16700 aerial photographs (for 1986) were used to compile an accurate map of the study area in the SSW. Care was taken to avoid erroneous plotting caused by the inherent distortion caused by the camera's lens towards the edges of aerial photographs. Orthophotograph maps are not available for the SSW or KNP yet. A 0,5 km^2 enumerated grid system, following the South African Co-ordinate System, was superimposed on the map.

The vegetation map demarcating the different plant communities (described previously) was superimposed on the map. Moreover, the original grid system was retained. As a result any specific location could be plotted, using the standard six-digit grid reference system. This allowed pinpointing any landmark to within 50 m^2. The field maps used were at a scale of about 1:20000.

When buffalo were located the exact position was determined and recorded by a grid reference. During the entire period of observation the grid reference together with references to habitat selection parameters, movements, physical parameters, and general activity were recorded at 20 min intervals on a Psion Organizer. The Psion Organizer is a battery driven mini-computer, with programme facilities and is able to hold a significant volume of data. These data are easily down loaded to a personal computer, thus saving the arduous task of transcribing hand written records to the computer.

AGEING CRITERIA AND FIELD AGE CLASSIFICATION

Fundamental to the study of the biology of an animal is the determination of criteria by which the age of the animal may be established. In the present study, these criteria were necessary for examining the age structure of the population and to assess social and spatial organization of age classes.

Determination of precise age of animals in the field is impossible unless the date of birth is known. In studies of behaviour it is usually unimportant to know the precise age of an animal, but recognition of age classes may be essential (Walther 1972).

Studies on the ageing criteria of African ungulates have been based largely on tooth and skull characteristics of specimens collected from natural mortalities and during culling programmes. Methods based on tooth growth and attrition have been reviewed by Morris (1972) and Spinage (1973), the latter with particular reference to Africa. Horn development as an index of age has also been widely used for various African ungulate species including the African buffalo (Pienaar 1969; Grimsdell 1973; Sinclair 1977), for which Simpson (1971) has also determined age classes in the field.

Ansell (1972) employed a method of field classification for antelope species based on height classes relative to the adult female. He used the following categories: infant, juvenile, sub-adult and adult. Ansell's field age criterion for infant, in which the height of the withers of the calf is compared to the adult female's elbow level, does not hold true for buffalo. The shoulder height of new-born buffalo calves (measured at the withers) varies from 76-81 cm, and the elbow level of adult females is rarely more than 70 cm above ground level (Pienaar 1969). A more reliable measure for separating the "infant" class, would be the imaginary line through the lingual fold at its highest point (91 cm above ground level) on the flank of the cow (Level A) (Figure 11). All calves of which the height at the withers falls below this line, may be reliably classed as infants. This would be a realistic classification as calves of greater shoulder height are usually weaned (five to six months old) and should really be classified with the next group, i.e. juveniles. A horizontal line (Level B), midway between the shoulder height (Level C) and the inguinal fold line (Level A) of adult females would separate juveniles from sub-adults, and here Ansell's criterion is valid enough for field application (Figure 11) (Pienaar 1969).

Of particular relevance to the present study are the studies of age determination and growth of African buffalo conducted by Pienaar (1969), Grimsdell (1973) and Sinclair (1977). Grimsdell and Sinclair in East Africa, both examined the same parameters as Pienaar in the KNP. These parameters included a number of horn, head and body measurements, body mass, changes in colour and texture of the coat and tooth eruption sequence and attrition. In addition attrition of the first molar tooth (M1) as well as age by counting cementum annuli in the first molar were quantified in east African populations. Moreover, Sinclair (1977), who compared growth characteristics of one South African and three East African buffalo populations, concluded that growth rates up to the age of three and a half years were very similar in all four populations.

The most useful field age classification systems have been provided by Pienaar (1969) and Grimsdell (1973), the former providing a description and a series of photographs of different age groups, while the latter provided a drawing of buffalo of various ages, with a scale based on attainment of asymptotic shoulder height (Figure 11).

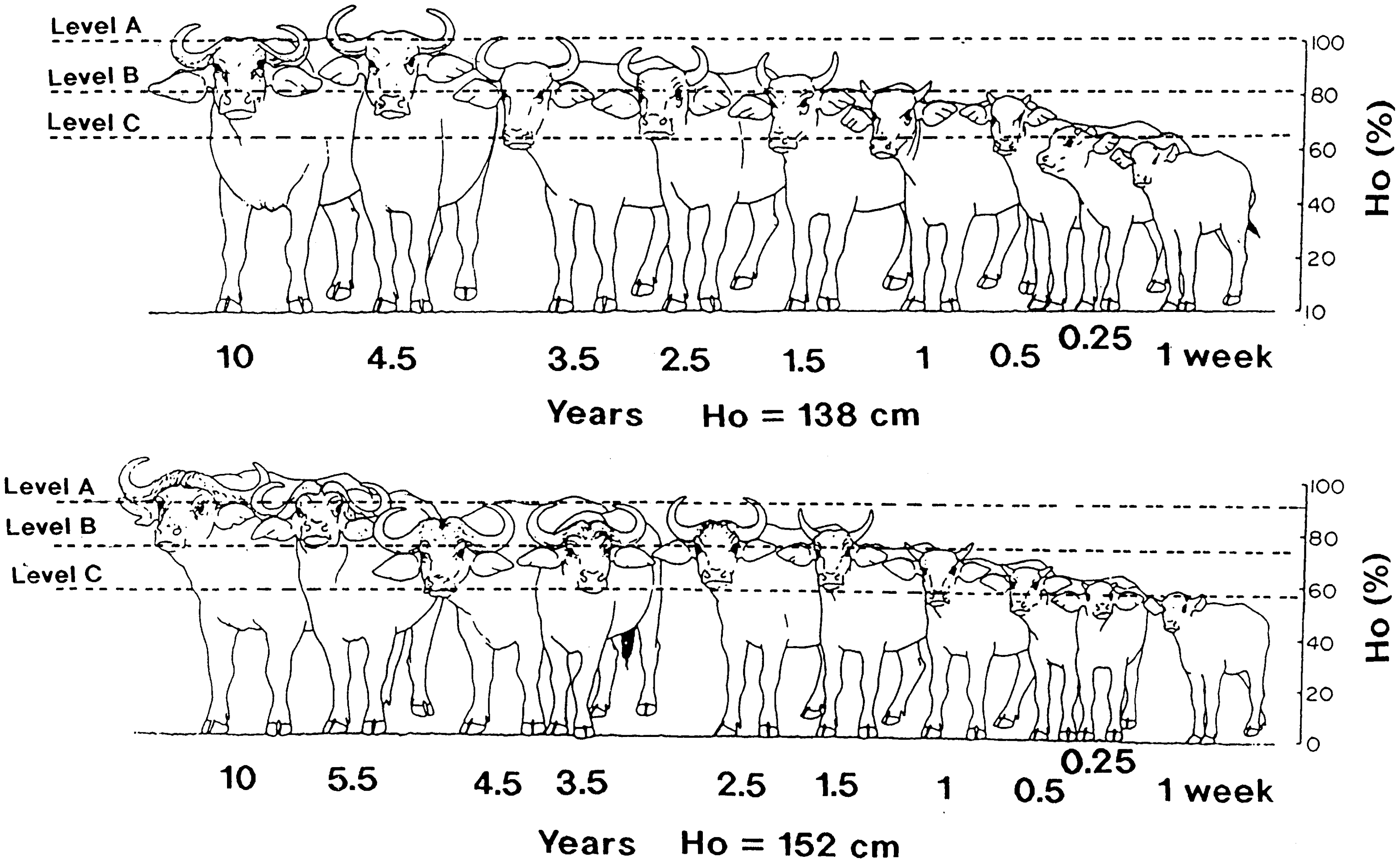


Figure 11. Field age classification a) female and b) male buffalo of various ages, drawn to a scale based on the attainment of asymptotic shoulder height (Ho) (Grimsdell 1973) and a modified version of Ansell's (1972) levels A, B & C.

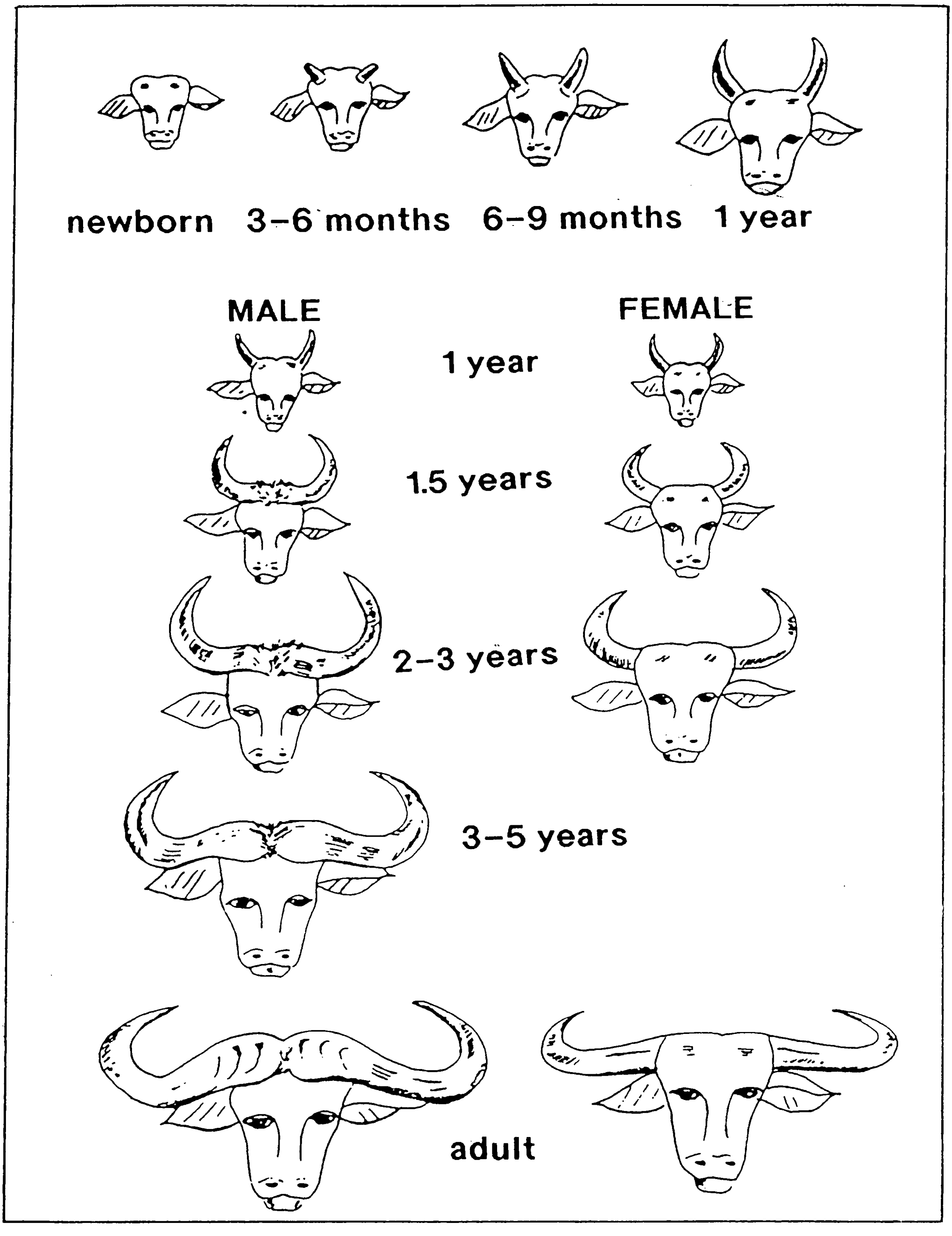


Figure 12. Field age classification for buffalo based on the shape and size of horns in the various age and sex classes (Sinclair 1977).

FIELD AGE CLASSIFICATION

From the outset classification in the field of age following Pienaar (1969) and Grimsdell (1973) was used in the study. Sinclair's (1977) method of ageing based on the shape and size of the horns (Figure 12), Grimsdell's (1973) method based on relative shoulder height (Figure 11), Pienaar's guidelines and Ansell's (1972) criteria were modified in order to provide a suitable age classification technique.

As births and neonates were only observed between early December and mid-April (4,5 months), ageing was greatly facilitated, since the youngest animal in the next age group was at least 7,5 months older and there was no overlap. This sharp delineation of age groups is most noticeable among younger age groups, but is still observable well into adulthood. Problems of erroneous age classification could be virtually eliminated during the period of mid-April to the beginning of December, as 99% of all animals observed were definitely within a well defined age group, e.g. calves less than twelve months, yearlings, two year old's, etc.

FIELD AGEING OF INFANTS:

This age includes the period from birth to some five months of age. During this phase active suckling occurs, but from about five months weaning takes place. Ageing criteria for this age group are as follows:

At birth (both sexes): Height at withers (76 - 81 cm) below "Level A". Colour black or dark olive-brown; smooth, silky coat and umbilical cord orange-red turning black.

2 weeks (both sexes): Height at withers (78 -84 cm) below "Level A". Horn buds visible, coat lighter, chocolate brown.

3 months (both sexes): Height at withers (85 cm) still slightly below "Level A". Short, clearly visible horns, coat colour now dirty yellowish-brown.

FIELD AGEING OF JUVENILES:

This category should include the period from 6 months old, onwards to the age of 24 months, but it is advantageous to differentiate further, thus the group only includes animals up to the age of 12 months. Ageing criteria for juveniles are:

6 months (both sexes): Height at withers (95 cm) just above "Level A". The horns (6 - 8 cm) straight, project up in shape of "V", coat remains same colour.

9 months (both sexes): Height at withers (100 cm) is well above "Level A". Horns are straight growing outwards and backwards, coat remains same colour.

Animals up to this age could be sexed only by their external genitalia, which was not always possible, especially when they were standing in long grass. However, the horns of juvenile males were slightly longer and wider than those of similar aged females.

FIELD AGING OF YEARLINGS:

This includes the period from 12 to 24 months. Sexual dimorphism becomes apparent, without having to refer to external genitalia, because of marked differences in nasal profile, horn and body confirmation.

Yearling males: Height at withers (103 cm at 12 months, 112 cm at 18 months) from half way to just below "Level B". By 18 months the horns are markedly curved, growing upwards and backwards with horn tips curving inwards. Horn length is about twice that of the ears, and they appear longer and flatter/wider than the females. The nasal profile is typically convex. The coat becomes darker and smoother.

Yearling females: Height at withers (106 cm at 12 months, 120 cm at 18 months) from slightly above "Level B" to midway between "Level A & B". Females slightly taller and longer than males. Horn length about 1,5 times the length of the ears, curving of the horns more pronounced than the males, but shorter and narrow.

The coat changes to a chocolate-brown. Nasal profile is typically straight.

FIELD AGEING OF TWO YEAR OLD'S:

2 year old males: Height at withers (119 cm) is about midway between "Levels B and C". the coat is chocolate brown and smooth, with yellow-brown only visible on the hindquarter. Horns grow in a semicircle outwards, upwards and the inwards, with average proportions as follows: length 65 cm; span 63 cm and the distance between horn tips 33 cm. Thickening of the horn base becomes noticeable, with hair loss over the rudimentary horn base (boss). The boy ridge which forms subcutaneously, supporting the developing boss, results in the facial profile no longer being straight (apart from the nasal profile which is already convex).

2 year old females: Height at withers (124 cm) is taller than that of males and is higher than the line midway between "Levels B and C". The coat is chocolate-brown and smooth with yellow-brown only visible on the hindquarter. Horns similar shape to those of the males, but shorter and narrower (length 43 cm, span 50 cm and distance between tips 31 cm on average). Nose and facial profile is flat. Body conformation is still relatively squarer than that of equal age males.

FIELD AGING OF SUB-ADULTS:

This includes the years from three to four years of age for males and females. Females above four years are classed as adults due to the fact that they start to breed, while males of this age are behaviourally more similar to young males, which never leave herds or show an interest in oestrus females. Older males, five years and older, do leave the herds temporarily in the winter, presummer and early summer months.

Sub-adult males: Height at withers (130 cm at three years, 136 cm at four years) halfway between "Levels B and C" of oldest males still present in the herd. The coat is uniformly smooth and dark chocolate brown, but slightly paler on the hindquarters. By four years the horns dip and widen further and approach the shape of adult males, but are not yet as wide as those of middle age males (6-7 years). On average the horn length is 90 cm; span 82 cm and tip to tip 47 cm. Considerable thickening of the horn base occurs. Flaking off at the horn tips in three year old's, is no longer seen in four year old's and the horns begin their backward sweep.

Sub-adult females: Height at withers (128 cm at three and four), is about the same as young adult females, but slightly lower than "Level C" of older females. The coat is uniformly smooth and dark chocolate brown. The adult shape of horn is attained, but they are not as wide and flat as those of middle aged and older females. The crown is well covered with hair (dissimilar to males), without a bony ridge, resulting in a flat facial profile. Ears are still remarkably intact.

FIELD AGEING OF ADULTS:

When recording sex/age data on the study herds of buffalo it was decided to classify all females over five years of age as adults. Due to the number of adult females, terrain and movement of the herd it usually not possible to distinguish between young, middle age and old females and, therefore, this was not done. The adult males, however, occurred in lower numbers than the females and were easily classed as young (5 - 7 years), middle aged (8 - 9 years) and old (>10 years) bulls. It was also important to know the approximate age of adult males because the middle and old age class bulls regularly move out of the breeding herd and associate with bachelor herds. Bulls above 11 years of age are classified as being very old and are never present in the herd.

Adult females: This group includes females from 5 to 10 years and older. The horns are wide, dipping lower than those of subadult females and are now characterized by their wide and flat span with widely separated horn tips. In very old females the horn tips may be blunt and worn down. There are from one to three distinctive post mature horn checks in middle aged cows, with more than four in old cows. The crown of the head shows signs of abrasion and hair loss, old females usually being bare. The face of old females, unlike those in middle age, is shrunken and bony, with a deteriorating physical condition, and the hips appearing bony. Young and middle age cows appear in better physical condition.

Young adult males: Height at withers from just above the midway line between "Levels B and C" (5 years) to the height at the withers of middle aged bulls (7 years). The horns have not quite attained their full width, the boss starting to loose its cover of hairy skin (5 years), with the horny layers of each horn growing forward around the boss (6 years) until they form a distinctive ridge but have not yet met completely in the centre of the skull, leaving a thin sparsely haircovered line across the boss (7 years). The boss itself although not showing any horn checks, becomes rougher. The ears are still quite intact apart from minor tears. The coat colour is very dark brown, changing to blackish-brown on the throat and neck, while the bigger skin folds in this area become slightly hairless.

Middle aged males: These males are big, but not as massive as old males. The boss is rough, frequently dented and showing post-mature horn checks, with no signs of hairiness remaining between the two horns, which have now met completely in the centre of the skull. Horn tips are showing slight wear. Coat colour is uniformly black, becoming hairless on the haunches and in most of the neck folds. The ears are frequently cut and torn.

Old adult males: These males are massive, and the biggest animals in the herd. Although the boss is still rough and dented with a number of post-mature horn checks, the dorso-central part shows excessive abrasion, becoming worn down and smooth. In very old males the boss and horn tips are often completely worn down or broken. The convex nasal profile is very pronounced. Ears are tattered and torn, while the body is marked by numerous scars. The areas above the eyes and on the cheeks are usually speckled by patches of grey-white hair, or entirely hairless. Large areas on the neck, belly and hindquarters become hairless, giving these males an overall greyish appearance. During the wet months they are invariably caked in mud.

Although the total number of criteria used to distinguish between the different sex/age groups was large, after some practice and observation, field ageing becomes natural and almost instantaneous. It is possible that a number of mis-classifications and overlaps occurred, but in general it is believed that, based on a number of criteria, the classification was consistent. Among the older age groups, particularly among adult males and females, a large proportion of the population was individually recognizable, thus excluding the possibility of multiple age classification on separate occasions.

INDIVIDUAL RECOGNITION

A prerequisite to the study of intraspecific behaviour patterns, spatial organization and monitoring herd sex and age structure and stability was the permanent individual recognition of a percentage of the animals. It was decided not to mark individual buffalo because it would be very expensive, time consuming and the Sabi Sand Management Committee had previously prohibited marking for aesthetic reasons.

The only alternative was to rely on physical characteristics and individual differences. The African buffalo presents a large variety of prominent individually specific features, such as horn shape, and the exact shape and location of cuts, scars bare patches and other marks on the face, ears and other parts of the body, which can be used for successful identification. Apart from individual differences, identification was greatly facilitated by the large number of sex/age groups, greatly reducing the potential number of animals per group which could have similar physical characteristics. Although a relatively high percentage of the study animals are known as individuals, this is not imperative to the ecological research being conducted. Knowledge of known animals, however, was used in evaluating the results of aggregation and dispersion, bachelor male movements and most importantly herd identification and monitoring. A reasonably large reference collection of names, sex and physical characteristics was set up. The total number of individually recognizable animals in each sex/age group is given in Table 5. It is also compared to the total number of animals in each sex/age group (separately for the Alicecot and Castleton sub-populations).

The high proportion of individually known adult cows and middle to old aged bulls, and the number of times they were resighted, provided for the collection of comprehensive information on their social behaviour and socio-spatial organization.

Table 5. Number of individually known animals per sex/age group in the study population. Number of known individuals are expressed as a percentage of all animals in that age group in December 1990.

Sex/Age group	Herd 1		Herd 2		TOTAL
	Number	%	Number	%	
FEMALES:					
Adult	21	30,0	5	7,1	26
Sub-adult	4	22,2	2	10,5	6
2 year old's	3	18,2	1	6,3	4
MALES:					
Old aged	1	100,0	1	100,0	2
Middle aged	5	71,4	2	28,6	7
Young adult	5	71,4	1	14,3	6
Sub-adult	9	37,5	4	17,4	13
2 year old's	7	41,2	2	14,3	9
Yearlings	2	14,3	0	0,0	2
TOTAL		57	18		75

CHAPTER 4: SOCIAL STRUCTURE/ORGANIZATION

INTRODUCTION

Leuthold (1977) defined social organization as being the result of all social interactions and spatial relations among the conspecific members of a population. Social organization includes such aspects as group types, group size, relations of individuals or groups to space, relations of individuals to each other, spatial and other relations between different sex and age groups, etc. While general aspects of the social organization tend to be species-specific, details are subject to considerable variation related to environmental conditions which often undergo cyclic changes (Leuthold 1977).

Behavioural relations between different sex and age groups, and specific individuals were to a large extent not a major component of this thesis. The social organization/structure of the SSW study herds were studied at the herd level, with particular emphasis on population size, sex/age structure, herd size and stability and the dynamics of bachelor male subgroups. It was felt that these studies would facilitate the interpretation of the ecological study of spatial utilization, including study of home range size, utilization of home range, habitat selection, spacing of herds, etc., dealt with in Chapter 5.

METHODS

POPULATION SIZE

Although not specifically an objective of the present study, an estimation of the total population size, within the confines of the study area, provided a useful framework and perspective for an interpretation of socio-spatial organization. The first total count of the buffalo living within the study area was made in July 1990. This count was subsequently verified during the annual census in August 1990, the buffalo population of the SSW being counted from the air with the aid of a helicopter. Total counts of the study herds were made whenever the opportunity arose, trying to count the herd at least once a month. The annual census of July 1991 was also used to confirm that the population estimates were indeed accurate. Estimates for the total population size for the SSW were obtained from the warden, for the period 1984 - 1991. These data will be analysed in Chapter 6.

In order to count the buffalo from the ground it was necessary for a number of conditions to be met. The herd should be on the move, it should be strung out in a long line almost in single file (not bunched), they should be moving at a constant slow speed and should be crossing an open area of veld where there were at least two landmarks (e.g. large trees or termite mounds) to use as markers. The observer then lines the markers up and counts only the buffalo that pass this line. These conditions are seldom met in the mixed woodland of the SSW, thus restricting the counting of herd size to suitable occasions. All the information that was available, from rangers, other members of lodge staff and personal observations were used to count and monitor the status and daily locations of bachelor male subgroups.

SEX AND AGE STRUCTURE

The classification of animals into different sex and age classes was accomplished at the same time as a herd count, all the prerequisites for a herd count applying, with one other condition. In order to classify the calves (0 - 12 months) as male or female it was necessary to view the external genitalia, thus the herd should be moving through open veld with a grass cover no higher than the lowest point of the stomach.

Observations were made with a pair of 10 x 25 field binoculars, the sex and age class of the individuals passing the marker line being verbally transcribed onto a dictaphone. The total number in the herd and numbers in each sex and age class being determined subsequently by analysis of the tape.

HERD SIZE AND STABILITY

The methods for estimating herd size have been described above. In order to determine whether or not these herds were comprised of a relatively fixed (stable) number it was necessary to monitor total herd numbers, increases in herd size due to reproduction, influx of males from bachelor groups, death of any individuals, etc. Changes in herd size due to fragmentation or recombination were monitored, as well as the interaction between large (>200) herds if they should meet. In all these observations reference was regularly made to recognizable individuals in order to confirm one's calculations. Accuracy was improved by making a large number of counts should any fluctuation occur.

If, for example, the herd (having x members excluding males $\geq$ 5 years) had been observed on day t, and a subherd (having y members excluding males $\geq$ 5 years and a portion of recognizable individuals) was observed on day t + 3, it is obvious that a split occurred in the preceeding two days, and furthermore, that in another area of the home range a subherd(s) of size x - y was to be found in the immediate vicinity, a count would reveal x - y members. If not, a further split had taken place, sometime between day t + 3 and the new observation.

In none of the above mentioned cases was it necessary to be present at the time of segregation, while the day of actual change could still be inferred with a high degree of accuracy, due to the high number of contacts with the groups (almost every day). Recombinations were treated in the same way.

The values, x - y, were never absolute, due to some misclassification, double counting and/or missing of hidden individuals. However, actual counts never deviated more than 4,2% from the expected number, and can thus be treated as an acceptable level of accuracy. Because adult males ($\geq$ 5 years old) frequently left herds to form bachelor male groups, simple arithmetic could not be used whenever the herd was divided into subherds, since all or some of the expected number of those males could either be in the other subherd, or else in bachelor groups. Therefore, inferred numbers had to be limited to those occasions where all subherds were fully counted and classified on the same day. When all subherds were combined it was possible to calculate the number of adult males not present in the herd at that particular time, based on the known number of adult males in the population.

BACHELOR MALE SUBGROUPS

The numerical status and age structure of the bachelor bull subherds was monitored as accurately as possible over the study period. Small variations were not as important as detecting the consequences of the calving and breeding season and subsequently the sexually inactive dry winter months. Regular movement of young and middle aged males in/ or out of the herds was monitored, as is described above.

As can be seen in Table 5, 100% of the true old aged bachelor bulls were individually recognizable, contributing to the accuracy of the monitoring program for bachelor males. Should adult males, normally confined to the breeding herd leave the herd it was recorded where these bulls went and which, if any, bachelor male subherds they interacted with.

RESULTS

POPULATION SIZE

The aerial census conducted by the warden and specific herd ground counts of the buffalo in the SSW in 1990, indicated the presence of around 1000 buffalo, in six breeding herds and 58 males in bachelor subgroups. The population had increased to an estimated 1160 in breeding herds and 71 as bachelors by July of 1991. The above results may be seen in Table 6, in which a breakdown of the numbers of buffalo living within the various herds is given. This increase from 1065 to 1230 buffalo in the SSW from 1990 to 1991 represents a 15,49% increase in one year. A group of 100 buffalo were also removed from the Wildtuin in the 1989-90 period.

There were two breeding herds in the study area, herd No.1 comprised 231 individuals and herd No.2 consisted of 219 buffalo in August of 1990. By August 1991 the herds had increased to 265 and 247 for herds 1 and 2 respectively. This represents a 14,7% increase for herd No.1 and a 12,8% increase for herd No.2. It can be seen in Table 7 how the total numbers in the study herd populations changed over the 14 month study period. The reasons for these fluctuations will be discussed later in this chapter.

A total of 401 sightings of buffalo groups were made and these ranged in size from lone animals to large herds in excess of 400 animals (when the breeding herd from the Mala Mala subpopulation moved into the home range of the Castleton/Ravenscourt population).

SEX AND AGE STRUCTURE

The frequency distribution of the sex and age classes of the mixed herds in the study subpopulations are summarized in Table 8 (Alicecot subpopulation) and Table 9 (Castleton/Ravenscourt subpopulation). The sex ratios in the age classes calves to subadults do not differ significantly from the expected 1:1 ratio. However, the adult age class presents a different picture, with adult males being out numbered by adult females by an average of 0,32:1. As can be seen in Figure 13 there was a very similar sex ratio between the two study herds.

From Table 10 it is evident that 96,15% of the total study population was found in the breeding herds in August 1991. This figure increased to 98,77% in February 1991 due to the influx of bachelor bulls in the breeding season. However, a large percentage (29,68%) of adult males that are part of the breeding herds left the breeding herds during part of the non-breeding season; however, they adapted only temporary bachelor status. Only 1,23% of the total population was permanently segregated from the breeding herds, these were very old males that could no longer compete with the younger middle aged to old bulls.

HERD SIZE AND STABILITY

Observations on herd size and stability revealed two major phenomena, namely:

(1) a continual fluctuation in the proportion of adult males (> 5 years old) in mixed herds, indicating that those males left and re-entered herds, and

(2) herd size remaining stable throughout the study period, with only slight fluctuations in size. No extended fragmentation was recorded, and only once did the study herds meet, although there was no mingling and the herd sizes remained the same.

Table 6. Total counts made of buffalo population in the Sabi Sand Wildtuin, for the July 1990 and July 1991 aerial census's.

Group counted	Location	Number 1990	Number 1991
Study herd 1	Alice/Castle	231	265
Study herd 2	Othawa/R/court	219	247
Breeding herd	Mala Mala	372	450
Breeding herd	Lisbon	142	151
Breeding herd	Toulon	26	27
Breeding herd	Arathusa	17	19
Bachelor males	Total for the reserve	58	71
Total for the reserve		1065	1230

Table 7. Total counts made of buffalo in the study area for the period August 1990 - August 1991.

GROUP COUNTED	MONTH Aug 90	Oct 90	Dec 90	Feb 91	Apr 91	Jun 91	Aug 91
HERD 1	231	226	225	255	271	266	265
HERD 2	219	218	218	229	258	249	247
BACHELOR MALES	18	17	17	6	9	19	22
TOTAL	468	461	460	490	538	534	534

Table 8. The sex and age structure of Herd 1 from August 1990 to May 1991.

AGE		MONTH						
CLASS	SEX	Aug 90	Oct 90	Dec 90	Feb 91	May 91	Jun 91	Aug 91
Calves	Female	20	19	20	14	24	23	23
	Male	25	23	24	12	22	22	22
Yearling	Female	13	13	13	19	19	19	19
	Male	14	14	14	23	23	23	23
2 year	Female	11	11	11	13	13	13	13
	Male	18	18	17	14	14	14	13
Subadult	Female	18	18	18	20	20	20	20
	Male	24	24	24	31	31	31	31
Adult	Female	71	71	70	79	79	79	79
	Male	15	14	13	23	22	22	22
Old male	Male	0	1	1	7	4	0	0
TOTAL		229	226	225	255	271	266	265

Table 9. The sex and age structure of Herd 2 from October 1990 to August 1991.

AGE		MONTH					
CLASS	SEX	Oct 90	Dec 90	Feb 91	May 91	Jun 91	Aug 91
Calves	Female	15	15	19	17	19	18
	Male	15	14	20	18	18	17
Yearling	Female	15	15	15	15	15	15
	Male	16	16	16	14	14	14
2 year	Female	16	16	15	15	15	15
	Male	14	14	14	16	16	16
Sub-adult	Female	19	19	18	24	24	24
	Male	23	23	23	25	25	25
Adult	Female	71	71	71	80	80	80
	Male	14	14	15	29	22	22
Old male	Male	1	1	3	5	1	1
TOTAL		218	218	229	258	249	247

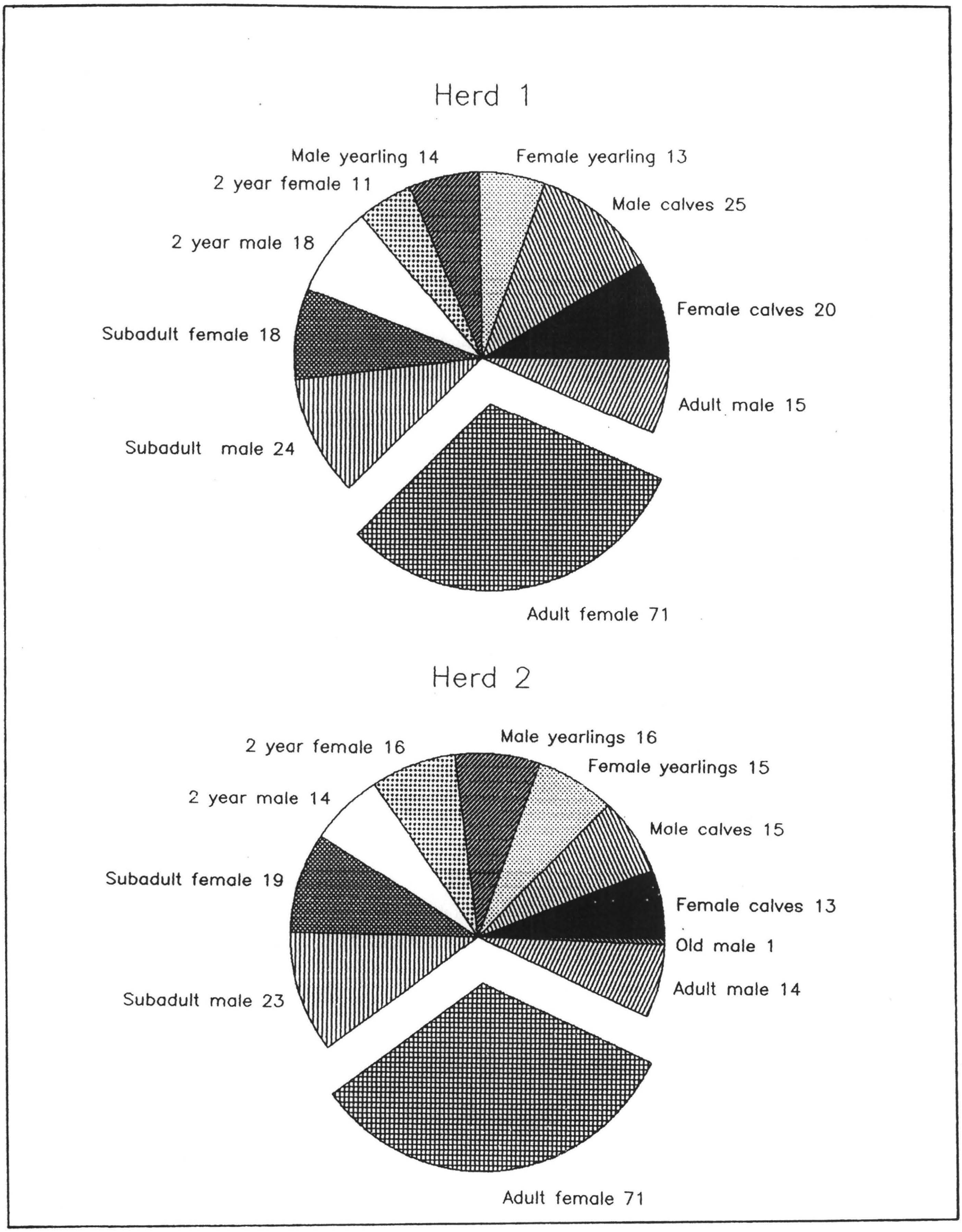


Figure 13. Pie charts to show the relatively similar sex and age ratios in a) study herd 1 and b) study herd 2 in October 1990.

Table 10. The proportions of the buffalo population in the study area groups within the study population.

BASIC SOCIAL GROUP	PERCENTAGE OF THE POPULATION Aug 90	Oct 90	Dec 90	Feb 91	Apr 91	Jun 91	Aug 91
Breeding herd	96,15%	96,31%	96,34%	98,77%	98,33%	96,44%	95,88%
Bachelor group	3,42%	3,25%	3,26%	0,41%	0,93%	3,18%	3,75%
Solitary male	0,43%	0,44%	0,4%	0,82%	0,74%	0,38%	0,37%

The number of individuals in each age class stayed relatively constant until January 1990, with the result that the herds remained as stable defined units. On occasions (n = 24) small groups (10-15 animals) strayed from the confines of the breeding herds. This was usually as a result of the presence of lions in the area, or after unfavourable weather conditions, especially high winds. These groups remained mobile and very nervous until they relocated the herd, scent and auditory senses being used. A less frequent (n = 3) cause of change in herd structure is a roughly equal split in the herd. This situation, however, has never lasted for longer than 24 h.

Aggregation of different breeding herds has to date not occurred. On a number of occasions, however, the situation has arisen where herds have been in close proximity, but have not actually interacted. Thus far, therefore, it seems as though the herds have a relatively stable composition, increasing in number due to new births and the influx of bachelor males in the breeding season (discussed in next section). Reasons for any decrease in herd numbers include death, individuals losing the herd and the exodus of old males to bachelor male groups in the nonbreeding months.

BACHELOR MALE SUBGROUPS

There were four semipermanent bachelor male groups in the area, the status of which varied as a result of the beginning of the breeding season, predation and the physical condition of the old adult males (see Table 11). A number of permanently solitary very old adult males occurred within the study area (Table 11).

In August 1990 there were 18 bachelor males in the study area. These occurred in four bachelor male groups and there were two solitary males. Although slight fluctuations did occur, the four groups remained relatively stable. The bachelor male population had declined by one individual to 17 by December 1990 due to lion predation. The number of bachelor males declined to six in February 1991, due to an influx into the breeding herds. By the middle of winter in August 1991 the bachelor male population had increased again to 24 individuals (see Table 11). 58 Bachelor males were counted during the aerial census of 1990. By August 1991 this number had increased to 71 individuals. This represents an increase of 22,41%.

DISCUSSION

POPULATION SIZE

These census figures, and those from 1984 until the present indicate the existence of six distinct sub-populations. Each sub-population contains at least one breeding herd, several bachelor male groups and solitary males. The Toulon and Arathusa herds, containing 27 and 19 individuals respectively, are small sub-populations, and which may develop into larger herds.

Although the population size and dynamics of the SSW buffalo population over the last ten years was studied at the reserve level, all the buffalo being taken into consideration. It was decided to concentrate the research effort on the two herds of buffalo that have their home ranges in the north west section of the reserve (see Chapter 2). Factors that influenced this decision included the availability of privately owned farms on which permission to traverse was granted. And, secondly because I already had some knowledge of the area and knew some of the landowners on a personal basis.

Chapter 6 concentrates on the population dynamics and post 1983/1984 drought response of buffalo in the SSW. The two study herds were looked at more intensively and were used to study finer details of the population such as fluctuations in mixed herd and bachelor male group sizes and the sex and age structure.

Due to the nature of the activity patterns and habitat selection of the bachelor male subgroups, it was not always possible to accurately monitor their movements, age structure or dynamics. It is felt, however, that the cumulative data collected over the study period present a relatively accurate picture of bachelor male life in the SSW over the annual cycle.

SOCIAL GROUPINGS

From these observations it was possible to distinguish three types of basic social groups. These are defined in Table 12. The term "basic social groups" implies that within some of these groups, further grouping based on sex/age did occur (not referred to at this stage).

The proportion of sightings of the different group types has no statistical significance, owing to the limited number of actual groups, necessitating deliberate searching of the same repeatedly seen groups.

No female was ever seen alone, however, at the beginning of the study there was a group of three to five bachelor males that for seven months were seen with two sub-adult females (one of three years and the other being four years of age). This association lasted until the Alicecot breeding herd (No.1) moved through the area inhabited by this group (to the north of the Sand river, near the western perimeter fence), after which the two sub-adult females and a five year old male joined the herd. This was the only case of females staying away from the breeding herd for an extended period of time. Groups of between 10 - 25 buffalo, including males and females, were seen on a number of occasions (n = 24). However, these were groups that had got lost from a breeding herd, and were very mobile in searching for the herd. In all other instances females were recorded to be part of mixed/breeding herds (n = 257).

Animals less than five years old, with the exception of those mentioned above, were invariably part of the mixed herds. Only adult males (over the age of five years) were recorded away from mixed herds. Young and middle aged adult males

Table 12. Definition and composition of the basic social groups observed among buffalo in the study area.

GROUP TYPE	DESCRIPTION
BREEDING HERD	Contains 17 - 450 animals of all sex/age classes, except very old males.
BACHELOR GROUP	Contains 2 - 8 animals, middle aged to very old males, some individuals may join herd to mate.
TEMPORARY GROUP	Contains 2 - 30 animals of all ages, that may combine with bachelor group, but always return to breeding herd.
SOLITARY	Always very old adult males, permanently solitary.

(5 - 7 years), when separate from mixed herds, always formed part of bachelor groups and were never seen singly (n = 31). They never remained permanent bachelors, but always returned to the mixed herds.

Older adult males were either recorded in mixed herds or in bachelor groups, or as solitary individuals. A proportion of them were only temporary bachelors, returning to the breeding herds. Only on 12 occasions were solitary old males seen to approach or enter the mixed herds, but this was always of brief duration (less than one hour). All of these observations were made in the months of March and April, when mating was at a peak. On entering the mixed herds, a massive old or middle aged bull would immediately chase the intruder and eventually drive him away, often inflicting injuries to the rump and hind leg as he chased the old bull away. With two exceptions (both individuals with severe leg injuries and limps), only males classified as "very old adult" were recorded as solitary (n = 25). They may, however, have associated with other solitary males or bachelor groups for brief spells (n = 9).

SEX AND AGE STRUCTURE

Notably the number of individuals in each age class stayed relatively constant until the end of December 1990, with few deaths occurring and little change in the adult male numbers. However, January and February showed some significant changes. There was the onset of the calving season, which necessitated that animals previously classed as calves were now classed as yearlings. The elevation to new age classes, therefore, was necessary throughout the age class spectrum (see Table 8 & 9). Other changes include an influx of bulls from bachelor male groups towards the end of February.

All age classes from calves to sub-adults revealed a sex ratio not deviating much from 1:1. The results of the chi-squared analysis of this data can be seen in

Table 13. Extensive observations on hunting lions in Botswana revealed that buffalo calves can form a large part of the lion's diet (McBride 1984), however, no kills by lions were recorded in the present study. On one occasion a leopard *Panthera pardus* was reported to have killed a newly born buffalo calf. Predation by lions or hyaenas may well have occurred, but was never observed, and may explain some of the reductions in numbers of calves through to sub-adults that occurred between herd counts. Prins (1987) found that there was some indication that juvenile mortality was higher in females than in males, as he found 67 sub-adult cows for 100 sub-adult bulls ($\text{Chi}^2 = 6{,}521$, $df = 1$, $P < 0{,}025$). In the present study, combining the sub-adults from herds one and two for December 1990, there were 37 sub-adult females for 47 sub-adult males ($\text{Chi}^2 = 1{,}191$, $df = 1$, $P < 0{,}500$). None of these data are enough to conclude that there is a significant deviation from the expected 1:1, but show that there is a tendency for there to be higher rates of mortality in females up to the sub-adult stage than in males.

The adult age class presented a different picture with adult bulls being significantly out numbered by adult cows (Herd 1: $\text{Chi}^2 = 37{,}333$, $df = 1$, $P < 0{,}001$; Herd 2: $\text{Chi}^2 = 36{,}465$, $df = 1$, $P < 0{,}001$). Mloszewski (1983) also found that herds of buffalo in East Africa contain fewer adult males than adult females. He found that the ratio of adult males to adult females can be as high as 0,9:1, the two sexes almost approaching numerical equality, or as low as 0,4:1. The present study on the mixed herds in the SSW, however, showed an even lower adult male to adult female ratio of around 0,32:1, the number of adult bulls being less than one third that of adult cows.

These differences in the adult male-to-female ratios can be explained due to a number of factors. First a proportion of the adult males stay away from the mixed herds in bachelor groups or as solitary individuals. Traditionally more males are killed by hunters, the male being a better trophy specimen than the female. There are, unfortunately, no accurate records of the number of adult buffalo males that have been

Table 13. To show that the sex ratios of the classes calves to subadults do not differ significantly from the expected ratio and that the adult class does differ significantly from 1:1.

Age class	Chi-square	DF	Significance level
Herd 1:			
Calves	0,364	1	P > 0,5
Yearlings	0,037	1	P > 0,5
2 year old's	1,286	1	P > 0,25
Sub-adults	0,857	1	P > 0,25
Adults	37,333	1	P < 0,001
Herd 2:			
Calves	0,035	1	P > 0,5
Yearlings	0,032	1	P > 0,5
2 year old's	0,133	1	P > 0,5
Subadults	0,381	1	P > 0,5
Adults	36,465	1	P < 0,001

hunted in the SSW over the last ten years, and it is, therefore, not possible to estimate the effect hunting has had.

It is also believed that there is differential predation on adult male buffalo by lions (Sinclair 1977). Prins (1987) found that the risk of predation for the adult sexes is different, with bulls running a significantly higher risk than cows (Chi^2 after Yates continuity correction = 22,88, df =1, P < 0,001). If we assume a sex ratio of 1 bull : 4,5 cows (as in Prins 1987 study), then Schaller's (1972) study in Manyara confirms the above hypothesis, as he reported 44 bulls being killed by lions and only six adult cows (Chi^2 after Yates continuity conversion = 159,18, df = 1, P < 0,001). The predation bias towards adult bulls does not extend to sub-adults, the sub-adult bulls and cows experiencing the same risk (Prins 1987). It is tempting to propose that adult males in bachelor groups, and especially solitary males, are at more risk to lion predation than those living in mixed herds, due to there smaller numbers. Prins (1987) estimates that adult males in mixed herds experience a risk only one third as great as adult bulls in bachelor groups.

Whyte (1990) continually monitoring buffalo in the KNP (and following on Joubert, Hall-Martin & Whyte 1986), suggests that the proportion of bulls in the population would be cyclical. As the buffalo in the SSW were under nutritional stress in the drought of 1983/84, so were those of the KNP. From culled buffalo in the KNP it was found that females were producing significantly more female than male foetuses (67 female:40 male {Chi^2 = 6,81; p = 0,01}). Under average rainfall conditions the reverse was found and more males than females were recorded. Before discussing this point any further I feel it is important to point out that foetal ratios of 63:44 (p = 0,63) or 64:43 (p = 0,04) would not have produced a significantly skewed sex ratio. It is with this knowledge that the ratios found by Whyte (1990) are relatively close to not being significant and the lack of sample size data and years of repeatability that one should carefully consider the following discussion.

The evolutionary significance of this, as well as the actual physiological mechanisms allowing for variations in the conception ratio of male or female foetuses, is not yet certain, but current theory (Clutton- Brook, Guiness & Albon 1982) proposes that for any individual in a population, it is of prime importance (in an evolutionary sense) to ensure that its genes are carried forward into the forthcoming generations by producing as many offspring as possible during its reproductive life.

For a buffalo cow it would seem that the best way to achieve this would be to produce male offspring, due to the higher potential number of offspring a male can sire. Male offspring place greater nutritional stress on their mothers, and in times of food shortage this may endanger the calf and the cow's life (Clutton-Brook *et. al.* 1982). A female calf in times of nutritional stress would be a better option, as it's chances of survival to reproductive age would be greater than a males.

Provided that more females than males are born to the buffalo population, then a gradual decline in the proportion of adult males (and eventually bachelors) would be expected. When one examines the sex ratios for the two study herds in the SSW, one notes that indeed there are more adult cows than adult bulls, and that this could reflect an increased rate of female conceptions in the drought years of 1983 to 1985. The veld in the last few years has received average rainfall, which could explain the shift to the expected 1:1 ratio. Until conclusive evidence of sex ratio modifications at conception are available one can only speculate on the above discussion as a possible reason for the skewed sex ratio, and indicate the necessity for longterm data sets needed to establish the validity of the hypothesis.

HERD SIZE AND STABILITY

One of the key questions posed at the beginning of this study was: "Do breeding herds contain subgroups/social units smaller than the herd?". As noted above, no lengthy herd segregation occurred during the study period. This is in contrast to the results of Kruger (1990) and Mloszewski (1983) who both found that buffalo herds underwent frequent fragmentation. That the buffalo herds observed in the present study should be very stable and not undergo fragmentation and subsequent recombination and those observed in the above mentioned studies do is rather puzzling. I believe the answer lies in the total sizes of herds and the presence or absence of subgroups or supergroups and their definition within the herd structure.

It was found that the two herds of buffalo that were observed did not seem to have subgroups or supergroups which when combined together, formed the herd. Mloszewski (1983), however, found, in a herd of 140 buffalo in southwestern Kenya, that there were three groups within the herd. Adult males were present in the groups, with adult females predominating. These groups were sometimes separated from each other by distinct breaks, while at other times they tended to merge. Even when the buffaloes were in a compact mass, the three groups did not mix with each other except around the edges. He subsequently observed this pattern in other herds and states that when the herd fragmented, these subherds remained essentially intact. He goes on to conclude that these subgroups appear to be the smallest self-contained social units of *Syncerus* and they vary in size from a very few animals, particularly in forest races, to possibly 100 in races of *S. c. caffer*, though most of them contain between 30 and 60 individuals. In water buffalo, with herds of 30 or more, family groups of 7 to 10 individuals can be distinguished (Tulloch 1967).

Unlike the results of Kruger (1990) and Mloszewski (1983), and in accordance with the results of the present study, Sinclair (1977) found no evidence for the formation of permanent subgroups in over 100 herds of buffalo in the Serengeti. He concludes that the smallest unit is that of an adult cow with a calf from the previous birth season and perhaps an older offspring of eighteen months. Grimsdell (1969) noted, in a herd of more than 100 individuals, that the members always remained together after mixing with and separating from adjacent herds, being clearly able to identify their own group. In the present study, on the two occasions when the two different study herds came into contact there was, however, no intermingling with the herds slowly grazing and walking apart from one another. A few bulls approached opposite herds, but no aggression was shown and they slowly moved back to the herds in which they were resident.

The SSW buffalo population crashed in the 1983/84 drought period. It is conceivable that the buffalo may have already been feeling the stress of the oncoming drought in the early eighties when Kruger (1990) was conducting his field work, and that these conditions led to the formation of supergroups within a herd or subpopulation, which in turn lead to more frequent fragmentation and recombination. One of Kruger's study herds was in excess of 800 buffalo, which could, purely through the size of the herd, stimulate supergroup/subgroup formation. This, however, does not explain the formation of three subgroups within Mloszewski's (1983) study herd of 140 buffalo. There may, however, have been other environmental variables at play in Mloszewski's (1983) study. Reports in the monthly records of the warden of the SSW in the 1983/84 indicate significant fragmentation of the breeding herds in the drought period with a dramatic increase in predation on the smaller groups by lions.

BACHELOR MALE SUBGROUPS

The situation with the bachelor male population is very interesting. Through identification and regular monitoring of herd structure and bachelor male group structure it has become apparent that bachelor male groups are very unstable, showing a strong seasonal bias in this instability. The proportion of bachelor males seen in the nonbreeding season was 3,85% in 1990 and 4,12% in 1991. However, when one looks at the proportions for the reserve as a whole one finds that 5,44% in 1990 and 5,77% in 1991 of the population occurred as bachelors. This compares with the figures found in other reserves, namely 5,9% in the Sengwa Wildlife Research Area in Zimbabwe (Conybeare 1980) and 6,98% in the KNP (Pienaar 1969); and 5,7% in Serengeti during the wet season in East Africa (Sinclair 1977).

This is of importance not only for academic reasons, the management committee of the reserve are also very interested to get information on sex/age ratios within the herds and specifically the status of adult males compared to adult females. Buffalo are prized trophy hunting animals and, in accordance with a philosophy of sustained utilization, it is necessary to know which buffalo can be removed without affecting breeding.

The results thus far show that the bachelor male groups remain relatively constant from June to January. Fluctuations in group size result from injury or the presence of lions. However, towards the end of January a high percentage of bachelor bulls in the middle to old age class joined the herds and establish their position in the dominance hierarchy. This is in accordance with the results of Grimsdell (1969), who found that the percentage of adult bulls within the breeding herds during the months of peak conception was about twice as high as that during months of little reproductive activity. The result was that the bachelor male groups dissipated, the only bachelor bulls to be found being groups of one or two from the old age class and often showing muscle injuries to the hind legs and quarters, presumably obtained in clashes with bulls from the herd.

The pattern of formation of bachelor male groups has reappeared in June 1991. However, these groups are of different sizes, utilize different home ranges and are comprised of different individuals. This further enhances their classification as being unstable, and leads one to ask if they are responsible for gene flow from herd to herd. Evidence to support this exists, due to the observation of some bulls associating with two herds.

These findings present the middle-aged bachelor bull as an important breeding class and certainly not as an outcast from the herd that should be made available to the trophy hunter. Due to selection of the riverine tributary woodland (see Chapter 5) and not having to walk the vast distances that the breeding herds do in search of food, I would like to propose that the middle aged bachelor male may be in better physical condition at the onset of the breeding season than bulls that stay in the breeding herds all year. This may give them a competitive advantage in establishing themselves in the mating hierarchy.

The 22,41% increase in bachelor bulls from 1990 to 1991 in the SSW is a good sign. However, if equal proportions in the rest of the Wildtuin are joining the breeding herds in summer as that found in the study area, then it would seem as if their numbers should be carefully monitored and the application of culling via trophy hunting restricted. At present the proportions of bachelors is roughly the same as that found in other areas. The middle aged to old bulls are important breeding animals, and the very old bulls which could be hunted often show quite marked horn attrition and are no longer such desirable trophies.

CHAPTER 5: SPATIAL ORGANIZATION/HABITAT SELECTION

INTRODUCTION

Buffalo are important members of the SSW herbivore community as their total biomass exceeds that of any other ungulate species and by their grazing and trampling can have far reaching effects on the vegetation. The SSW is a restricted area being fenced, and as such cannot be a natural system/ecological unit in which buffalo populations must, therefore, be managed. For this reason, regular monitoring of the buffalo population has been carried out by the management staff of the SSW. This is accomplished via an annual census, during which most of the larger mammal species occurring in the SSW are counted from a helicopter, which flies evenly spaced flight lines to reach a total estimate. The estimates for buffalo herd sizes are obtained by analysis of aerial photographs of the herd, and ground counts (as described in Chapter 4). The results show a steady increase in buffalo following the population crash in the 1983/84 drought.

The buffalo population has increased to over 1100 individuals and the management committee of the SSW has begun to introduce population control measures in response to fears that the food requirements of the buffalo population may be excessive, especially in drought years. In accordance with a policy of sustained utilization of a renewable resource. it is important that the population should not be so large that in a dry period too many valuable animals are lost. It is hoped that some of the results of this essentially academic study of the ecology of the savanna buffalo in the SSW, will be applicable to the management of the SSW, and other southern African buffalo populations.

HABITAT SELECTION

A sound knowledge of the habitat requirements of ungulates within a game reserve is imperative for the formulation of management policies. Another of the key questions in this section was "Does the distribution and movement of buffalo function to maximize utilization of the best available habitat?"

This question essentially summarizes the direction that the project expanded in. The two breeding herds in the study area seemed to have defined home range's, but with considerable overlap. For logistical reasons I decided to concentrate data collection on the herd of 271 animals in the western section of the study area. The study herd was observed on a daily basis: movements, habitat selection and environmental data being collected daily. A more complete look at the parameters being recorded on a daily basis and hourly while observing the buffalo is given in Table 14.

In order to answer the above question the first step was to determine whether there was any preference or avoidance of particular habitats, and also whether there was any variation in habitat selection between seasons. As described above, data on habitat selection were collected daily over a 15 month period. This allowed sampling in the winter months of 1990 and 1991, the presummer months of 1990 and 1991 and the summer period from October 1990 to March 1991.

DISTRIBUTION, MOVEMENT PATTERNS AND HOME RANGE

One of the key questions in this section was "Do buffalo herds show a fixed pattern of range utilization?". Buffalo home ranges have been measured in East Africa by Sinclair (1977) by radio telemetry and Grimsdell (1969), Leuthold (1972) by observation only; and in southern Africa by Conybeare (1980) using radio telemetry. These estimates will be compared with those found for the study herd of buffalo in the SSW. These authors, however, did not look at areas of concentrated use within the home range, which has been analysed in this study. Comparisons of habitat types from East Africa to those southern Africa were taken into account when analysing any differences that were found.

Harris, Cresswell, Forde, Trewella, Woollard & Wray (1990) defined a home range as consisting of a more or less restricted area within which an animal moves when performing its normal activities. However, as an individuals range may change over time, the period for which it is measured must be specified in order for the measurement to be meaningful. The exact size and shape may have little significance in themselves, as they may be largely dependent on the method used to determine them. Alternatively, they may be closely related to factors such as population density, intra- or interspecific interactions and resource abundance and distribution (Sanderson 1966, King 1975, Cooper 1978, Waser 1979, Kruuk & Parish 1982, Wolton 1985, Carr & Macdonald 1986, Harris *et. al.* 1990, Hewson & Hinge 1990, Horner & Powell 1990, Ortega 1990)

Animals rarely utilize their potential habitat in an entirely random or uniform manner. Departures from random or uniform distribution may result from non-uniformity of habitat, in terms of resource distribution or impassable terrain, or from attraction to, or avoidance of, other animals (Brown & Orians 1970, Samuel, Pierce & Garton 1985). The clumped or patchy use of areas within a home ranges requires analyses that emphasize internal structure of home ranges and not merely outlines or total area measures (Horner & Powell 1990). Disproportionate space use creates areas of concentrated use, or "core areas" which Samuel *et. al.* (1985) defined as an area where space use exceeds that expected from a uniform distribution. As with home ranges, the size and location of a core area will be dependent upon the method used to determine it.

DAILY ACTIVITY PATTERNS

The quality of food available to the buffalo declines during the dry season relative to the previous wet season (Sinclair 1977, Taylor 1985, Prins 1987). There is also usually a decline in the available surface drinking water, although in the SSW the high number of artificial water sources and the Sand river ensure a continuous water supply (throughout the year).

Savanna buffalo graze predominantly in the cooler daylight hours and at night, but spend similar proportions of time ruminating during the night and the day. In all, some 85% of the 24 h is taken up with grazing and ruminating (Sinclair 1977). In this section, I consider whether the buffalo adjust to the resource restrictions during the dry season in terms of altering their daily activity patterns and specifically their timing of grazing and ruminating within the 24 h period.

Table 14. Habitat selection parameters recorded in the field on the Psion Organizer. Codes and classes were developed and used in the field.

Parameter	Example
Date	Mon 3 Jun 1991
Time	09h38
Grid reference	265130
Habitat type	RTW - Riverine, tributary woodland
Soil type	ACS - Alluvial silt, black clay or sand
Type of landscape	STU - Strongly undulating
Position in landscape	RBE - Riverbeds
Slope	6 - 2-6 degrees
Direction of movement	NE - North east
Wind direction	SE - South east
Wind strength	5 - Gentle breeze (0-5 knots)
Percentage cloud cover	40 - 21-40%
Distance from water	1000 - 0,5-1,0 km
Percentage grass cover	100 - 81-100 %
Density of vegetation	5 - very thick vegetation
Leaf table height	60 - 41-60 cm
Flowering culm height	80 - 61-80 cm
Grass growth stage	FGD - Flowers dead/leaves green
Level grazed	TLF - Top leaves/flower
Distance moved since Last observation	1000 - 0,5-1,0 km

METHODS

HABITAT SELECTION

A useful means to determine the statistical validity of habitat selection data is a chi-square test of the hypothesis that the buffalo herd use the different habitats in proportion to their availability to the herd, a multinomial distribution. A problem in using this test arises when the null hypothesis is rejected and a significant difference between the "expected" and observed frequency of use is observed. The chi-square does not determine preference or avoidance of individual categories, so the data must be inspected to determine which observations contribute most to the calculated chi-square value, and whether a specific type is preferred or avoided (Neu, Randall Byers & Peek 1974). In order to do this, Bonferroni confidence intervals were used (Neu *et. al.* 1974, Randall Byers, Steinhorst & Krausman 1984, Griffith & Peek 1989) and a level of significance of 95% experiment-wise confidence intervals on the proportional use of each habitat type for each season. The Bonferroni statements hold without reference to the initial significance of the chi-square test or whether or not it has been conducted.

In his study on the buffalo in Kenya, Sinclair (1977) used an adaptation of Cole's (1949) coefficient of association to statistically analyse habitat selection. Cole (1949), in considering a method for measuring the association between species of animals, pointed out that normal correlation techniques cannot be used because the frequency distributions of organisms in samples commonly differ widely from a random distribution. As this is the case with buffalo, Cole, therefore developed formulae which would give a measure of association ranging from +1 to -1, these being the maximum possible positive and negative associations respectively, and zero represented random association. Association in the statistical sense is defined by Cole as "the amount of co-occurrence in excess of that to be expected if two categories are independently distributed".

In this study many grid squares contained two or more habitat types and it was, therefore, decided to determine a coefficient of association by dividing the chi-square value for each habitat with the sum of chi-squares for that season. These values could be plotted on the same + or - graphs used by Cole to get an index of habitat selection. This formula was used in conjunction with the Bonferroni confidence intervals analysis in the present study in order to get comparable results with those of Sinclair (1977). This measure of association does not assume a bivariate normal distribution, gives a linear measure of magnitude of association, allows the use of small numbers of observations and generates measures of significance using the chi-square technique.

DISTRIBUTION, MOVEMENT PATTERNS AND HOME RANGE

A number of naturally marked (horn shape, split ears, body markings, etc) animals permitted a relatively large number of individuals within a herd to be identified easily (see Table 5), which in turn allowed repeated identification of the same herd of buffalo. Its movements were determined by locating it daily, or nearly daily, by tracking and monitoring movement patterns. Tracks on reserve roads and those followed in the veld helped in reconstructing nocturnal and unobserved daily movements. The data recorded and recording techniques used in these observations are described in Chapter 3.

The suitability of a number of techniques, commonly used to analyse home range or radiotracking data, were considered: minimum convex polygons, grid cells, probalistic methods, harmonic means, core convex polygons and cluster analysis.

Minimum convex polygons

(Voight & Tinline 1979, Macdonald, Ball & Hough 1980, Kenward 1987, Mykytka & Pelton 1988, Harris *et. al.* 1990).

To produce a minimum convex polygon the outermost locations are joined to form the smallest possible convex polygon. This method, however, can greatly overestimate the size of the home range because it includes all recorded locations, some of which may be unusual excursions outside the normal area of activity and thus includes large areas not actual used by the animal. Although several methods have been proposed to reduce the inclusion of these non-utilized areas, these are all somewhat arbitrary and therefore not acceptable. Information on intensity of space use within the home range is also not shown. Advantages of the technique include the fact that it can be used even if only a small number of locations are available, it is unaffected by autocorrelation data and due to its simplicity it is the only technique that is strictly comparable between studies.

Grid cells

(Siniff & Tester 1965, Adams & Davis 1967, Macdonald *et. al.* 1980, Kenward 1987, Saltz & Alkon 1989, Harris *et. al.* 1990).

Home range sizes can be calculated using grid cells, although this method usually requires some modification which limits its accuracy and objectivity. It is, however, useful for describing the intensity of range use and for the analysis of habitat use and conspecific interactions. The suitability of this method to a particular study depends on the size of the grid squares used and thus the accuracy of the analysis. In their simpler forms grid cell analyses have the advantage of being able to be carried out by hand without the necessity for computers.

Probalistic methods

(Ford & Krumme 1979, Voight & Tinline 1979, Macdonald *et. al.* 1980, Wolton 1985, Kenward 1987, Mykytka & Pelton 1987, Harris *et. al.* 1990).

Probalistic methods attempt to assess an animals probability of occurrence at each point in space and thus produce a theoretical home range for an average animal of that species in a uniform environment. The various probalistic methods all make one or more of the following assumptions:

1. The animals use of space will be normally distributed around a single, centrally placed centre of activity.
2. All locations are independent, i.e., not autocorrelated.

Consequently, most probability circles or ellipses bear little relation to an individual's real pattern of space use and are thus unsuitable for analysing home range and shape, intensity of space use, habitat use or conspecific interactions

Harmonic means

(Dixon & Chapman 1980, Wolton 1985, Kenward 1987, Mykytka & Pelton 1987, Harris *et. al.* 1990).

Harmonic means use the first inverse moments of locations to estimate activity centres and range use contours. They can identify multinuclear centres of activity and the contours, or "isopleths", can be set to include varying proportions of locations. However, the use of a mathematically derived centre of activity, which in some cases may have little biological significance and upon which all other calculations are based, is unsatisfactory. Clusters of locations are not treated separately and thus isolines may fail to match the real distribution of locations, either being drawn towards concentrations of distant locations or by contouring around large unused areas. Additionally, if the distribution of locations is highly skewed, if there are a large number of outlying locations or if too few locations are available, the home ranges calculated may be highly inaccurate. Despite the above criticisms, this method can provide a useful analysis of some data sets, particularly those comprising a large number of locations. Harmonic means are relatively unaffected by the auto-correlation of data but the use of different algorithms in the various computer programs available make accurate comparisons between studies difficult

Core convex polygons

(Mohr & Stumpf 1966, Kenward 1987)

Core convex polygons are created by progressively excluding the locations which are furthest from the range centre so producing probability contour polygons. The range centre may be defined as a resting site or some other such focal point, or may be mathematically derived by a variety of methods, none of which necessarily have any biological significance. None of the methods of defining the range centre are particularly satisfactory in most cases, and this method is not suited to the analysis of multinuclear ranges.

Cluster analysis

(Kenward 1987, Harris *et. al.* 1990)

Cluster analysis uses hierarchical incremental cluster analysis with a nearest neighbour joining rule to draw contours which include varying proportions of locations. It makes no prior assumptions about the shape of a range or about the distribution of use within a range and clusters are treated separately. It may, therefore, be used to analyse multinuclear ranges, those with a skewed distribution of locations or those having a large number of outlying locations. Like the harmonic mean method, cluster analysis is relatively insensitive to auto correlation data but also has the disadvantage of different algorithms making comparison between studies difficult.

For the reasons outlined above, cluster analysis was chosen as the main method of home range analysis. Kenwards (1987) "Program 2" was used, as modified by Dott (H.M. *pers. comm.*), using data collected during the study period. Not only does cluster analysis provide a satisfactory method of analysing space use patterns but it enables the results to be presented in a clear and interpretable manner. The minimum convex polygon method, although of limited value, was also used for the reason of it's simplicity and comparability with other studies.

As Macdonald *et. al.* (1980) pointed out, "...without knowing the answer one cannot predict how appropriate a given estimate will be." Therefore, the contours used to define a home range or core area were not predetermined but were chosen according to which produced the most meaningful analysis of the data. Range use was therefore classified as follows:

1. <u>Total home range (THR)</u>

   Defined by the minimum convex polygon (= 100% cluster). Although often containing large areas not used by the herd, the THR is taken to represent the potential home range of the herd during the specified period and includes temporary exploratory excursions.

2. <u>Normal home range (NHR)</u>

   Defined by the 95% contour, i.e., the cluster, or clusters, containing 95% of the locations, the NHR is taken to represent the areas used by the herd during the course of its natural activities

3. <u>Area of intensive use (AIU)</u>

   Defined by the 80% contour, the AIU approximates to the core areas of the home range.

DAILY ACTIVITY PATTERNS

Activities of individuals within the herd were recorded every 20 min during observation periods, using the standard scan sampling technique, following Jarman & Jarman (1973), who found that it was difficult to distinguish and keep one individual in view for extended periods; and Bernstein (1991) who gives merit to *ad libitum* scoring techniques when the sole objective is to produce large bodies of data without regard to absolute or relative frequencies. Mean values were obtained for lengths and patterns of activities. The sampling intervals used were 20 min periods, to ensure that the buffalo within the herd were given ample opportunity to change activities between successive scan samples.

Observations were made from a vehicle to which they were habituated and which allowed a vantage position from within the herd. Observations were made with 10 x 25 binoculars and recorded on a Sony M-740 microcassette recorder. When scanning the herd the activity of each animal was recorded, starting from left to right. Of the various behaviour elements recorded, only grazing, walking, drinking, standing, resting and ruminating are considered here. If ruminating, an animal either stood still or rested on its brisket. In the latter position the head was slightly raised, and this could be distinguished from the resting position, in which the chin was close to the ground. Resting occurred infrequently, only for a few minutes at a time, as is typical of large bovids (Balch 1955, Mloszewski 1983).

Rhythmic variations in behaviour are found in many species, and can be detected using various methods of analysis (Martin & Bateson 1986). The technique used in the present study was to plot the frequency of various activity patterns at hourly intervals in the various seasons.

RESULTS

HABITAT SELECTION

The number of observations and percentage of the total observations for the various habitat types in the different seasons are summarized in Table 15. Using the chi-square test it was found that for all three seasons there was significant ($p < 0,05$) selection against utilization of the available habitats in proportion to occurrence. The chi-square statistics to prove this are summarized in Table 16.

As can be seen in the table there has been a reduction in the number of habitats from the original 17 described in Chapter 2, to the 10 different habitats used in this analysis. This reduction was done in order to reduce the number of variables in the chi-square calculation. Airstrips and rock outcrops were combined to form a group called "Other (OTH)" as they contributed to only 1,52% of the study area. Sand savanna (SSU) and sand savanna - cleared (SSD); mixed tree savanna (MTS) and mixed tree savanna - cleared (MTD); knobthorn red turf savanna (KTR) and knobthorn red turf savanna - cleared (KTD); *Euclea* thicket mosaic (CBT) and *Euclea* thicket mosaic - cleared (CBD) and riverine thicket woodland (RTH) and riverine woodland - cleared (RWC) were lumped as they were the same habitats, but have been modified recently by man. Riverine and tributary woodland (RTW) and riverine floodplain (RIF) were also lumped as they occur along the river systems.

Bonferroni confidence intervals were calculated to determine whether the various habitats were selected for or rejected (Table 17 - 19). A plus sign in the table means the habitat type was positively selected for (0,05 level of significance) during that season. A negative sign means that the habitat type was utilized less often than the proportion with which it occurred (0,05 level of significance). And no sign means that the habitat type was utilized in equal proportion to that with which it occurred. Figures

14a - 14c show a numerical and a visual representation of the coefficients of association for the buffalo herd and the various habitats in the three seasons.

The results of monitoring the proportions of the various browse species consumed in the diet of the study herd of buffalo, as revealed from scan sampling, are given in Table 20.

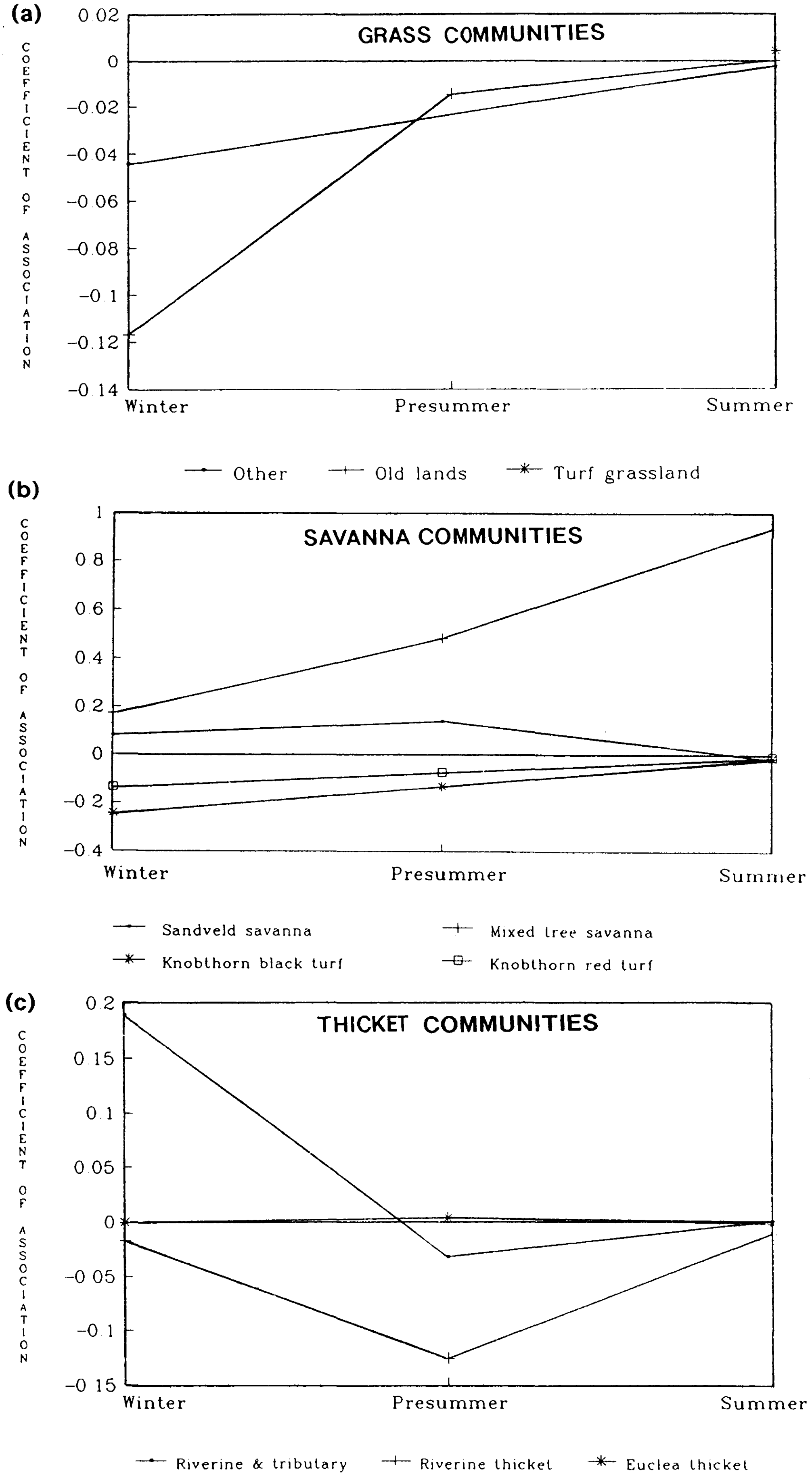


Figure 14a - 14c. The coefficient of association for the buffalo herd and the various habitats in the three seasons.

Table 15. The number of observations and percentage of the total number of observations in the various habitat types for the three seasons.

HABITAT TYPE	WINTER Number	%	PRESUMMER Number	%	SUMMER Number	%
RTW	74	15,13	15	5,98	28	4,14
OFL	8	1,64	8	3,19	39	5,75
OTH	2	0,41	-	-	2	0,30
SSU	278	56,35	161	64,14	199	29,40
MTS	48	9,82	40	15,93	355	52,43
KTB	12	2,45	5	1,99	14	2,07
KTR	11	2,24	5	1,99	11	1,62
RTH	39	7,96	7	2,78	18	2,66
CBT	17	3,48	10	3,98	8	1,18
TGL	-	-	-	-	3	0,44

Table 16. The chi-square statistics with regards to seasonal selection of various habitat types.

Habitat	Winter			Presummer			Summer		
Type	Obs.	Exp.	Chi.	Obs.	Exp.	Chi	Obs.	Exp.	Chi
RTW	15,13	9,43	3,44	5,98	9,43	1,26	4,14	9,43	2,96
OFL	1,64	4,86	2,13	3,19	4,86	0,57	5,76	4,86	0,16
OTH	0,41	1,52	0,81	-	-	-	0,30	1,52	0,97
SSU	56,35	48,00	1,45	64,14	48,00	5,42	29,40	48,00	7,20
MTS	9,82	5,62	3,13	15,93	5,62	18,91	52,43	5,62	389
KTR	2,45	8,66	4,45	1,99	8,66	5,13	2,07	8,66	5,01
KTB	2,24	6,15	2,48	1,99	6,15	2,81	1,62	6,15	3,33
RTH	7,96	9,70	0,31	2,78	9,70	4,93	2,66	9,70	5,10
CBT	3,48	3,29	0,01	3,98	3,29	0,14	1,18	3,29	1,35
TGL	-	-	-	-	-	-	0,44	2,76	1,95
Total			18,24			39,21			417,9
Degrees of freedom			8			7			9
Significance			p < 0,05			p < 0,001			p < 0,001

Table 17. Proportional availability and use of various habitat types by buffalo in the study area from July 1990 and winter 1991, selection determined by Bonferroni confidence intervals.

Chi-squared = 18,2428 with 8 d.f.

Significance < 0,05 - reject null hypothesis at 95% level

Habitat type	Total km^2	A (Pto)	B	C	D (Pi)	Confidence interval on proportion of occurrence
RTW	15,98	0,094	74	6,98	0,1513	0,1060 ≤ Pi ≤ 0,1960 +
OFL	8,24	0,048	8	0,39	0,0164	0,0003 ≤ Pi ≤ 0,0317 -
OTH	2,57	0,015	2	0,03	0,0041	0,0000 ≤ Pi ≤ 0,0119 -
SSU	81,37	0,480	278	133,44	0,5685	0,5070 ≤ Pi ≤ 0,6310 +
MTS	9,53	0,056	48	2,70	0,0982	0,0607 ≤ Pi ≤ 0,1351 +
KTB	14,68	0,086	12	1,04	0,0245	0,0054 ≤ Pi ≤ 0,0445 -
KTR	10,43	0,061	11	0,68	0,0224	0,0038 ≤ Pi ≤ 0,0409 -
RTH	16,45	0,097	39	3,78	0,0797	0,0452 ≤ Pi ≤ 0,1136
CBT	5,58	0,032	17	0,56	0,0348	0,0118 ≤ Pi ≤ 0,0577
TOTAL	169,51	1,0000	489		1,000	

A (Pto) - Proportion of total kilometres squared

B - Number of times buffalo herd observed

C - Expected number of buffalo herd observations

D (Pi) - Proportion observed in each habitat type

Confidence interval determined at 95% level

Table 18. Proportional availability and use of various habitat types by buffalo in the study area from presummer 1990 and 1991, selection determined by Bonferroni confidence intervals.

Chi-squared = 39,2097 with 7 d.f.

Significance < 0,01 - reject null hypothesis at 99% level

Habitat type	Total km²	A (P*to*)	B	C	D (P*i*)	Confidence interval on proportion of occurrence
RTW	15,98	0,0943	15	1,42	0,0598	$0{,}0572 \leq Pi \leq 0{,}0624$ -
OFL	8,24	0,0486	8	0,39	0,0319	$0{,}0151 \leq Pi \leq 0{,}0623$
SSU	81,37	0,4800	161	77,28	0,6414	$0{,}5585 \leq Pi \leq 0{,}7243$ +
MTS	9,53	0,0562	40	2,25	0,1594	$0{,}0961 \leq Pi \leq 0{,}2227$ +
KTB	14,68	0,0866	5	0,43	0,0199	$0{,}0000 \leq Pi \leq 0{,}0441$ -
KTR	10,43	0,0615	5	0,31	0,0199	$0{,}0000 \leq Pi \leq 0{,}0441$ -
RTH	16,45	0,0970	7	0,68	0,0278	$0{,}0000 \leq Pi \leq 0{,}0562$ -
CBT	5,58	0,0329	10	0,33	0,0398	$0{,}0006 \leq Pi \leq 0{,}0736$
TOTAL	169,51	1,0000	251		1,000	

A (P*to*) - Proportion of total kilometres squared

B - Number of times buffalo herd observed

C - Expected number of buffalo herd observations

D (P*i*) - Proportion observed in each habitat type

Confidence interval determined at 95% level

Table 19. Proportional availability and use of various habitat types by buffalo in the study area from October 1990 to March 1991 (summer); selection determined by Bonferroni confidence intervals.

Chi-squared = 417,974 with 9 d.f.

Significance < 0,01 - reject null hypothesis at 99% level

Habitat type	Total km^2	A (P*to*)	B	C	D (P*i*)	Confidence interval on proportion of occurrence
RTW	15,98	0,0943	28	2,64	0,0414	0,0199 $\leq$ P*i* $\leq$ 0,0629 -
OFL	8,24	0,0486	39	1,89	0,0576	0,0324 $\leq$ P*i* $\leq$ 0,0828
OTH	2,57	0,0152	2	0,03	0,0030	0,0000 $\leq$ P*i* $\leq$ 0,0089 -
SSU	81,37	0,4800	199	95,52	0,2939	0,2448 $\leq$ P*i* $\leq$ 0,3430 -
MTS	9,53	0,0562	355	19,95	0,5244	0,4700 $\leq$ P*i* $\leq$ 0,5779 +
KTB	14,68	0,0866	14	1,21	0,0207	0,0055 $\leq$ P*i* $\leq$ 0,0365 -
KTR	10,4311	0,0615	11	0,68	0,0162	0,0134 $\leq$ P*i* $\leq$ 0,0289 -
RTH	6,45	0,0970	18	1,75	0,0266	0,0090 $\leq$ P*i* $\leq$ 0,0455 -
CBT	5,58	0,0329	8	0,26	0,0118	0,0108 $\leq$ P*i* $\leq$ 0,0132 -
TGL	4,68	0,0276	3	0,08	0,0044	0,0000 $\leq$ P*i* $\leq$ 0,0108 -
TOTAL	169,51	1,0000	677		1,000	

A (P*to*) - Proportion of total kilometres squared

B - Number of times buffalo herd observed

C - Expected number of buffalo herd observations

D (P*i*) - Proportion observed in each habitat type

Confidence interval determined at 95% level

Table 20. Browse selection by buffalo in closed sand savanna woodland in the three seasons in the study area, SSW.

Plant species consumed	Number of times recorded Summer	 Winter	 Presummer
Black monkey orange - *Strychnos madagascariensis*	-	-	4
Common false-thorn - *Albizia harveyi*	-	13	56
False currant resin - *Ozoroa insignis*	-	-	8
Red bushwillow - *Combretum apiculatum*	-	5	21
Round-leafed kiaat - *Pterocarpus rotundifolius*	2	12	143
Russet bushwillow - *C. hereroense*	-	3	23
Sickle bush - *Dichrostachys cinerea*	-	-	11
Silver raisin - *Grewia monticola*	-	7	17
Weeping bushwillow - *C. collinum suluense*	-	-	12
Weeping wattle - *Peltophorum africanum*	-	3	11
White raisin - *G. bicolor*	-	2	19
Forbs	2	9	35

DISTRIBUTION, MOVEMENT PATTERNS AND HOME RANGE

In order to compare the seasonal utilization of the entire home range it was decided to determine home range size in the different seasons. Figures 15a - 15c show plotted locations of the herd in the three seasons, with the THR, NHR and AIU estimates of home range, for the study herd in the winter, presummer and summer seasons. Movement patterns within the seasonal home ranges were quite different, these patterns are summarized in Figures 16a and 16b.

The results of monitoring movements patterns (distances covered) over the 24 h cycle are summarized in Table 21. In terms of daily movement, this mainly occurred at night, with average nocturnal distance covered being greater than diurnal distances (see Table 21). The mean distance covered by a group of buffalo in a 24 h period varied from season to season (Table 21).

The home range estimates are based on 1765 locations for herd No.1, 1256 of which were location sightings and 509 of which were determined from following spoor. Taking the seasonal utilization of different areas of the home range, and those areas occasionally visited by the buffalo herd under consideration, a year round total home range of approximately 120 km^2 was obtained. The mean size for herd No.1 was taken as 248, this corresponds to a minimum density of 2.07 buffalo per km^2. The overall density estimate for buffalo within the SSW was 2,16/km^2.

DAILY ACTIVITY PATTERNS

A total of 1350 (450 winter, 540 summer, 360 presummer) scans of activity patterns within the herd were conducted, a further 1256 recordings of general herd behaviour were made while taking habitat selection recordings.

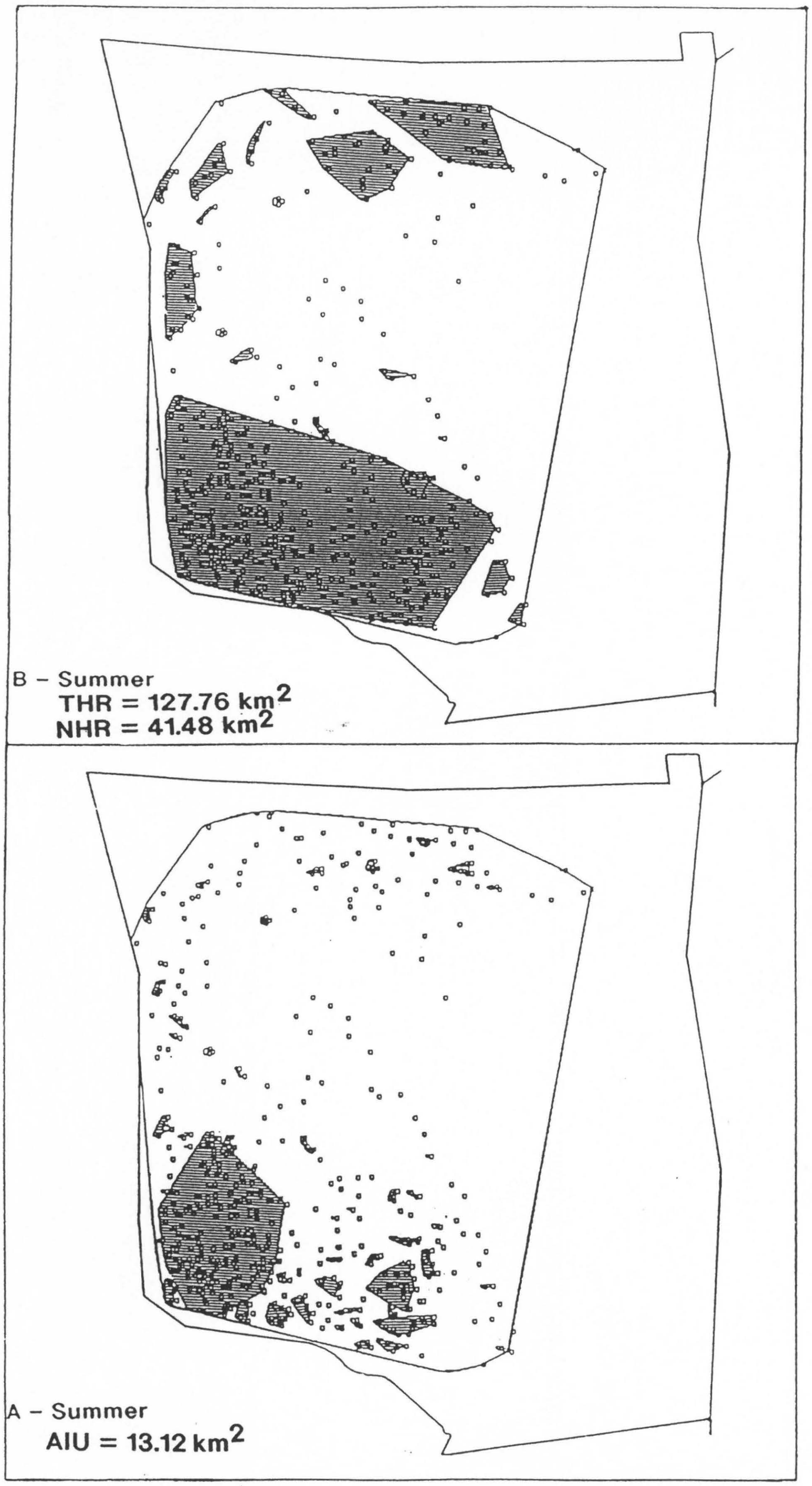


Figure 15a. Home range size as determined by total home range (THR), normal home range (NHR) and area of intensive use (AIU) for the summer season.

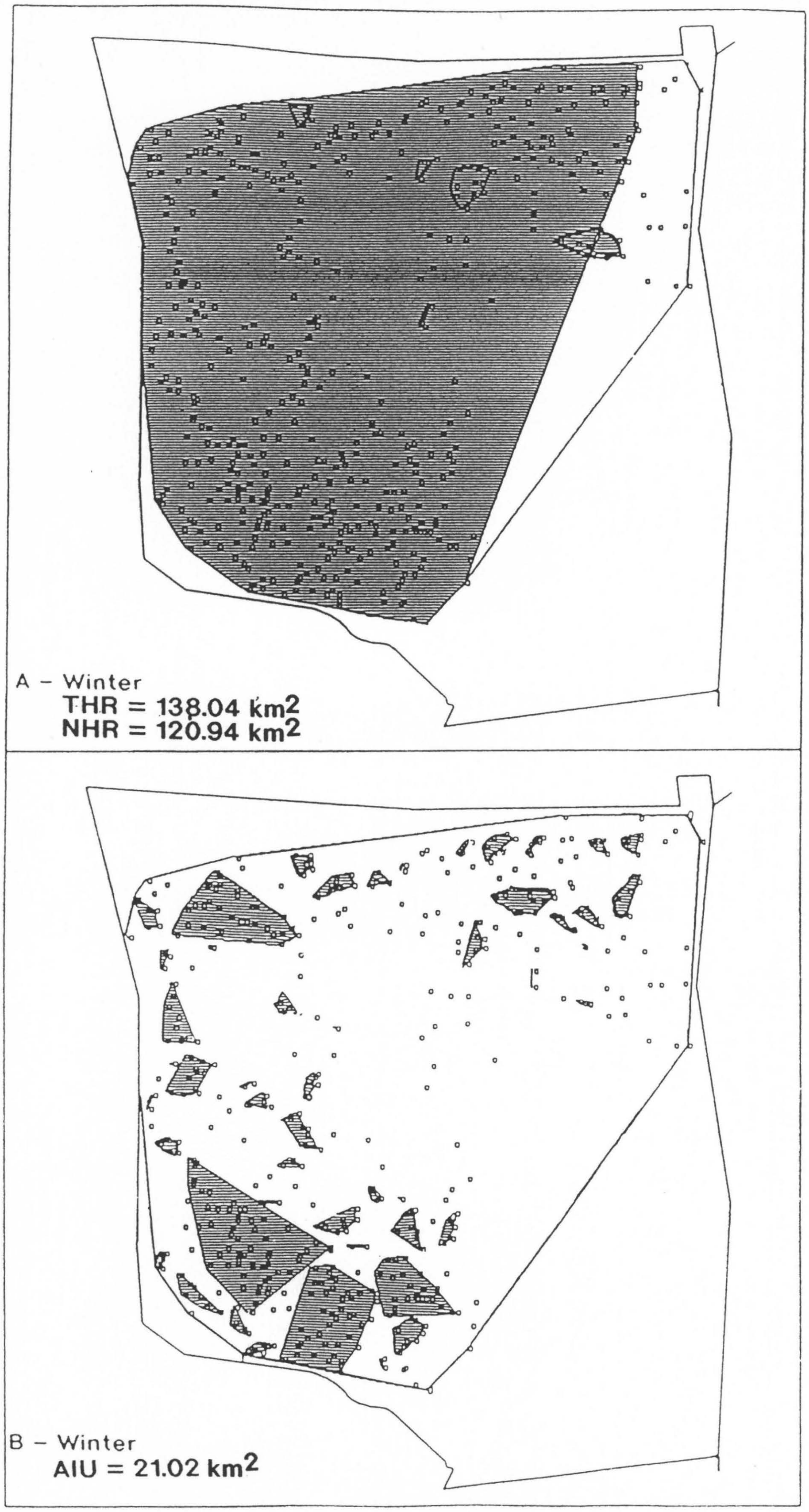


Figure 15b. Home range size as determined by total home range (THR), normal home range (NHR) and area of intensive use (AIU) for the winter season.

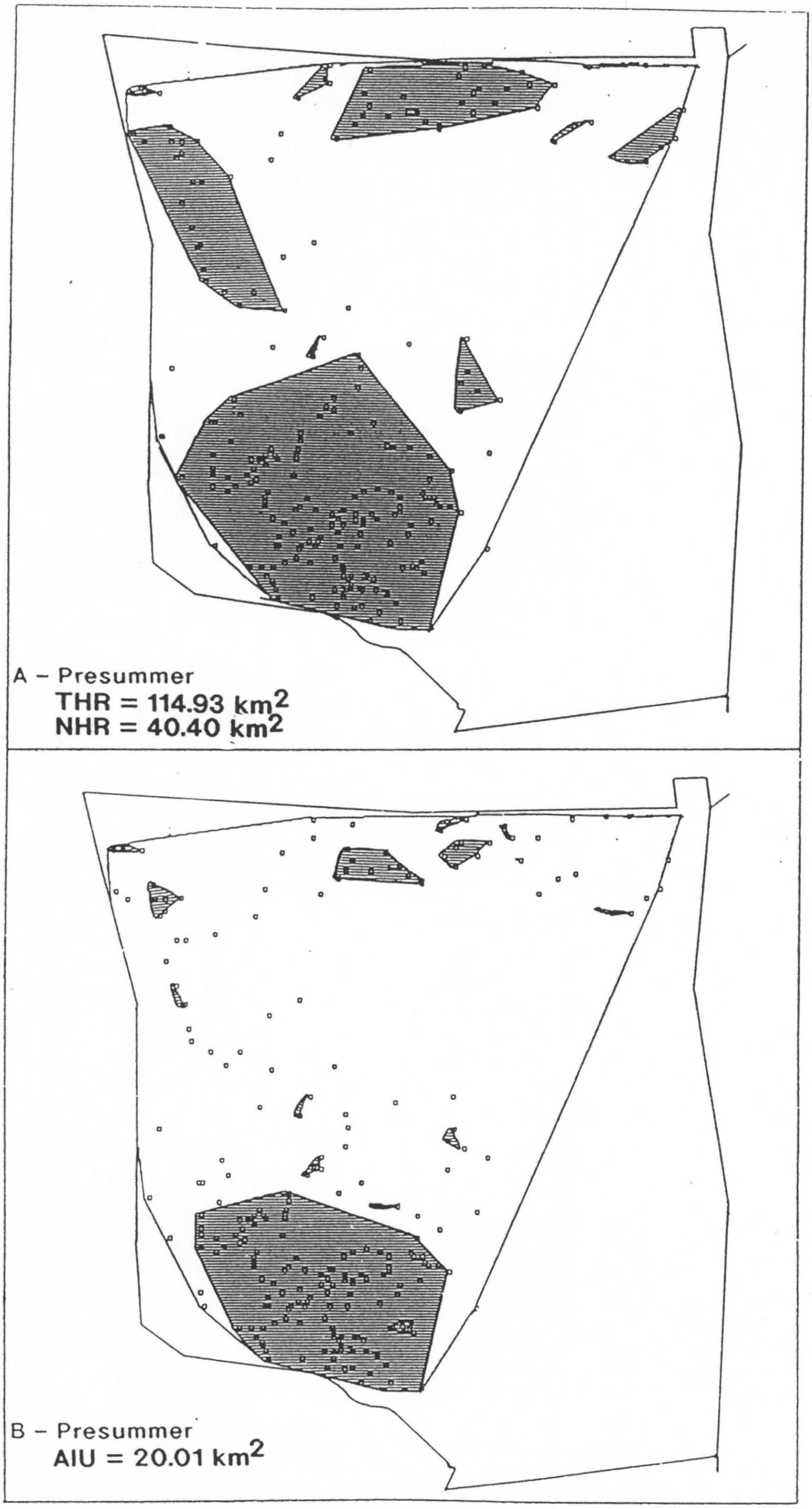


Figure 15c. Home range size as determined by total home range (THR), normal home range (NHR) and area of intensive use (AIU) for the presummer season.

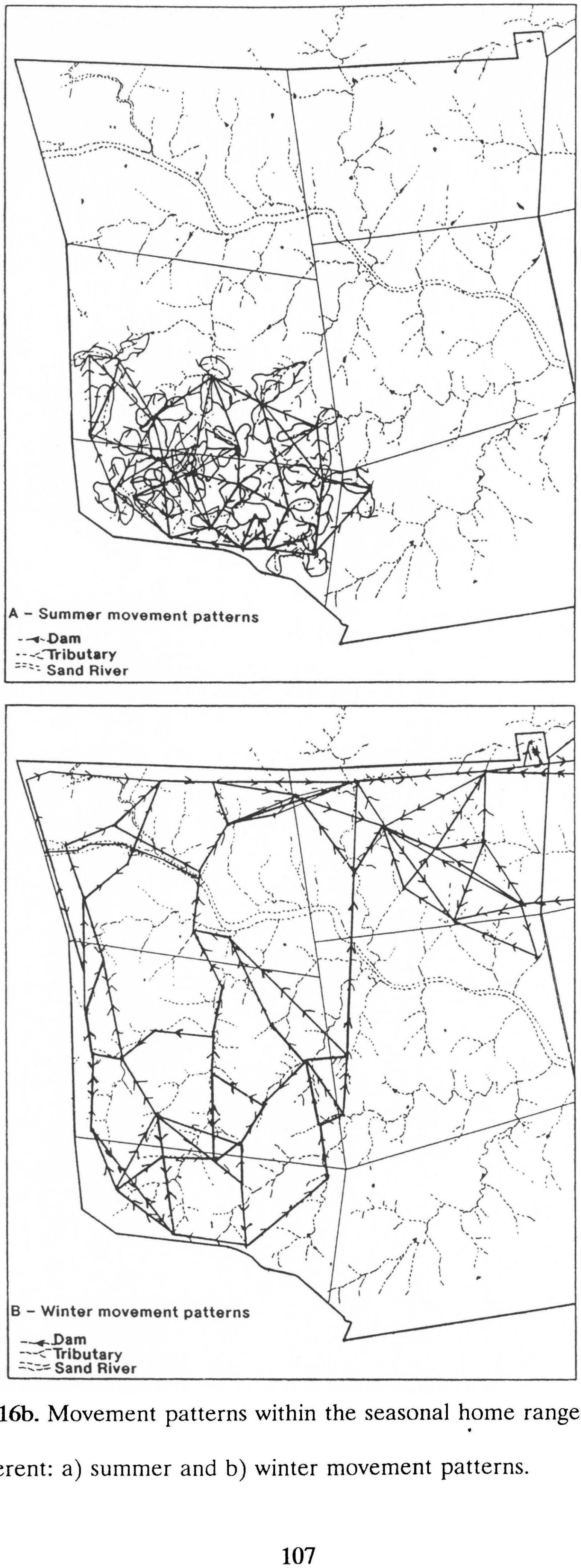


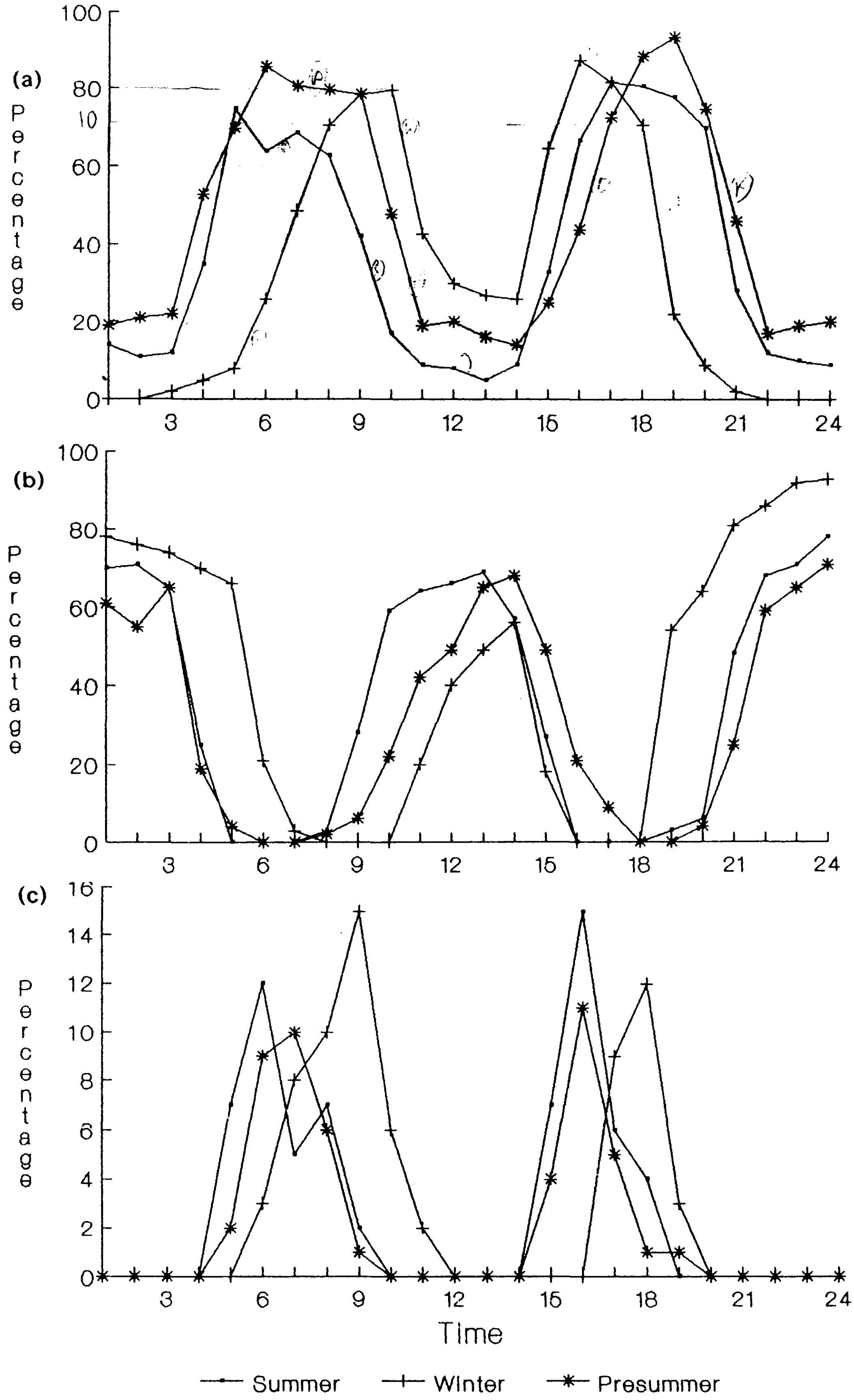
Figure 16a & 16b. Movement patterns within the seasonal home ranges were quite different: a) summer and b) winter movement patterns.

It was, therefore, possible to determine what proportions of the day were spent in specific activities, and the timing of these activities.

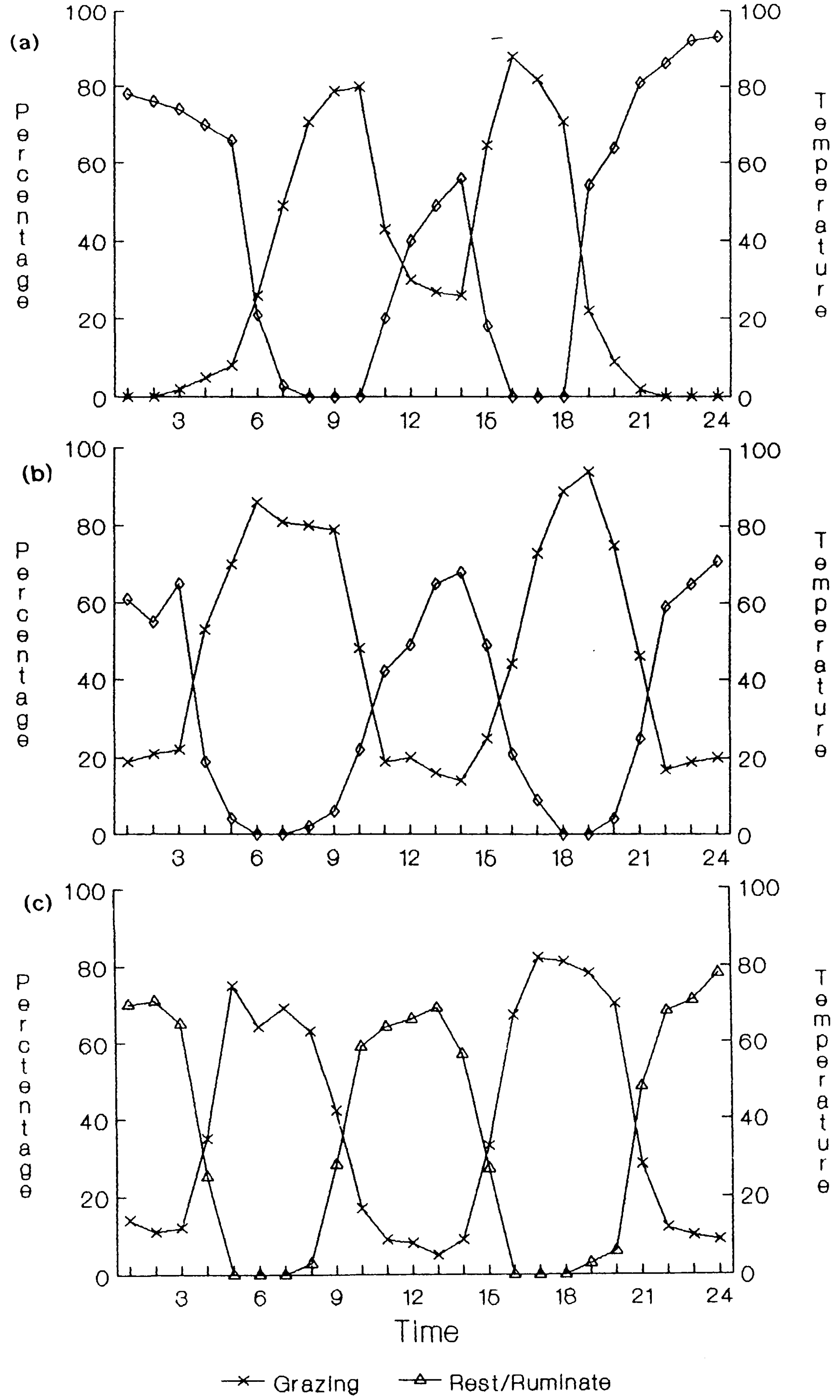
The locations shown in Figures 15a - 15c generally represented the daytime resting locations, somewhat clustered along the sandveld ridges (cleared and undisturbed), where tree communities afford shade conditions. Usually the herd was feeding in the early morning, from 04h00 up to about 09h00 in the summer and from 04h30 up to about 10h30 in the cooler winter months (Figure 17a and Figures 18a - 18c). Then resting most of the day until 16h00 - 17h00 in the summer and 15h30 - 16h30 in the winter (Figure 17b and Figures 18a - 18c), when they resumed feeding again and started to move quickly towards water. The herd usually drank in the early morning and late afternoon/early evening in all three seasons (Figure 17c). The proportions of social interactions observed in the scan sampling for the three seasons are summarized in Figure 19.

Table 21. The results of monitoring movement patterns (distances covered) over the 24h cycle for the various seasons. Also includes differences between daily and nocturnal movement patterns for the various seasons.

Season	Mean distance covered		
	24 hour cycle	diurnal movements	nocturnal movements
Summer	3250 m	1225 m	2075 m
Winter	6455 m	2750 m	4015 m
Presummer	2955 m	1310 m	1745 m



Figures 17a - 17c. Mean proportions of each hour in the 24 h cycle spent a) grazing, b) resting/ruminating and c) drinking at a waterhole by the study herd in the seasons summer, winter and presummer.



Figures 18a -18c. The inverse relationship between the mean proportions of each hour in the 24 h spent grazing or resting/ruminating, in a) winter, b) presummer and c) summer.

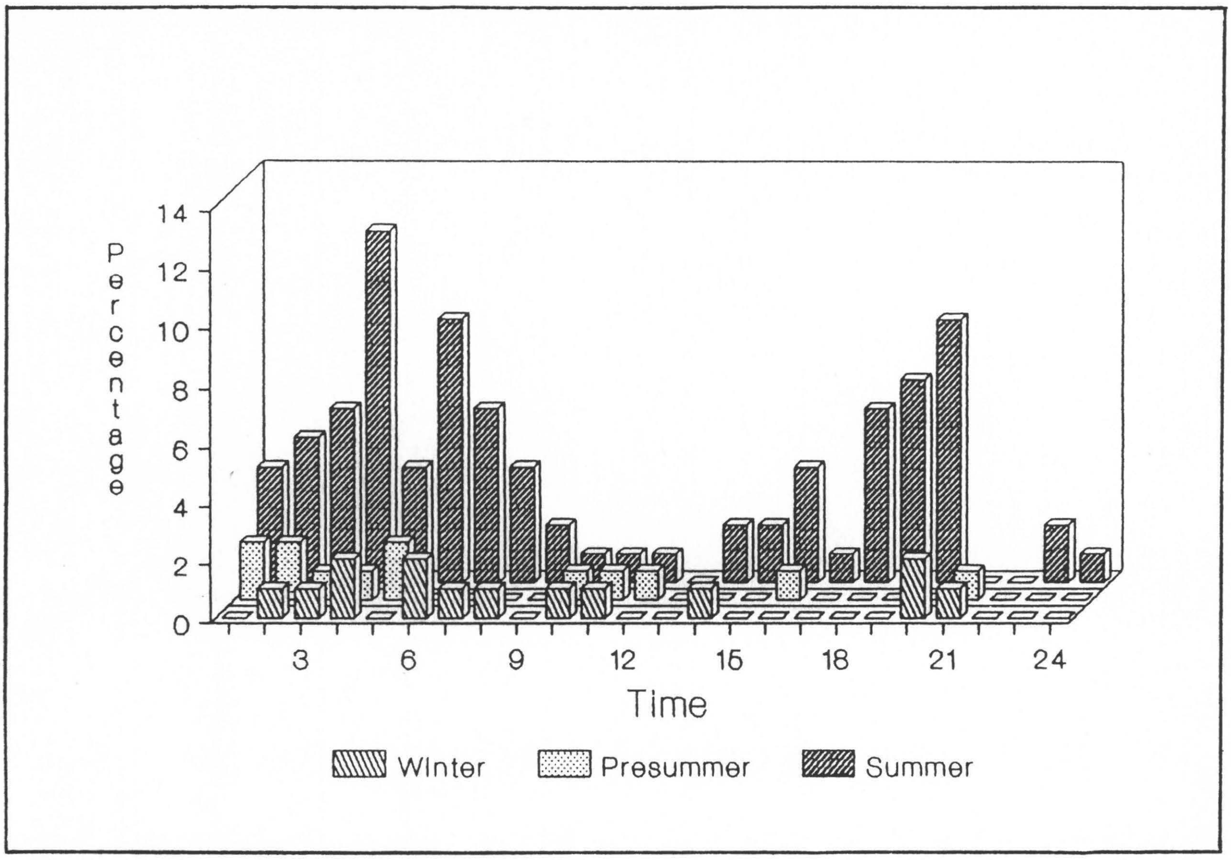


Figure 19. The proportions of each hour in the 24 h cycle spent in social interactions in summer, winter and presummer.

DISCUSSION

HABITAT SELECTION

From the results presented it is possible to draw some conclusions with regards to habitat selection by the study herd in the SSW over a sixteen month period of average rainfall. At the first level it was shown that in all seasons the buffalo did not show a random utilization of the available habitat types in the study area in proportion to their percentage occurrence. The significance levels for these statements were $p < 0{,}05$ in winter and $p < 0{,}01$ in both summer and presummer (Table 16). It, therefore, became evident that the buffalo were showing some selection for particular habitat types and rejection of others.

The Bonferroni confidence intervals that were determined, using the chi-square statistics, showed that there was indeed positive selection for some habitats, rejection of others and that some were utilized in proportion to their percentage occurrence. The analysis also showed that the selection/rejection of particular habitat types showed some seasonal variation (Table 17 - 19). The chi-square statistics were also used to determine coefficients of association (COA), in order to quantify and give a visual representation (Figures 14a - 14c) of the selection and/or rejection and to determine which habitats were more important to the buffalo and whether there was any seasonal variation.

From the data presented in Figures 14a - 14c it can be seen that the grass communities were generally selected against. The turf grasslands where ignored completely in the winter and presummer seasons, with selection in proportion to availability in the hot, wet summer months following the *T. triandra* grasslands green flush, especially if the TGL areas were burnt in the presummer months. During the winter months the COA for old lands sand savanna was -0,12 and for other (airstrips and rock outcrops) was -0,04. Both OFL and OTH were determined to be selected against in the Bonferroni analysis. These figures, although negative, are not far from zero and especially in the case of OTH may not be the result of rejection by the buffalo, as particularly airstrips were often crossed in regular movement paths.

As can be seen in Table 4 the forage potential for OFL was determined to be medium, although there was a high fuel potential. Therefore, although a relatively high biomass (2541 kg/ha) of available forage existed in the winter months, the veld had equal proportions of DEC and INC II grass species and did not offer the best available grazing (see text Chapter 2, and Table 4). In the hot presummer the OFL areas were used in proportion to their occurrence (Table 18), while the biomass remained relatively high (Table 4). No records of buffalo herds in TGL and OTH were made in the presummer. In the summer the Bonferroni confidence intervals determined that OFL was utilized in proportion to its occurrence and that TGL and OTH were rejected, although the COA for all these habitat types were almost zero.

Therefore, it has been shown that the buffalo herd under study did not select for open grassland, that in the winter months they selected against these areas and, although the Bonferroni estimate says not, that the COA's show that these grasslands were utilized almost in proportion to their occurrence in the study area during the presummer and summer months.

The utilization of the savanna communities by the buffalo was quite different. In the cool, dry winter undisturbed sandveld and mixed tree savanna's were positively selected for by the buffalo (Table 17). These habitats were determined to be both high in terms of their forage and fuel potentials (Table 4). Both these habitats had high proportions of palatable DEC grass species, although in both the proportion of INC II grass species was relatively high, indicating some over utilization of these areas. The COA's for these habitat types were 0,1 and 0,2 for SSU and MTS respectively. The records for MTS and cleared mixed tree savanna (MTD), and SSU and cleared sand savanna (SSD) were combined in order to determine the chi-square, Bonferroni and COA's. The winter biomass estimate for MTS and MTD being 2344 kg/ha and 2400 kg/ha respectively were both relatively high and were, therefore, favourable areas for the buffalo to graze in. A high percentage (56,35%) of the observations of the buffalo in winter were made in the SSU and SSD habitat type (Table 15), which constituted 48% of the study area and where biomass estimates of 2390 kg/ha and 2218 kg/ha respectively were measured (Table 4).

The red and black knobthorn turf savanna areas were both negatively selected for in the winter, with COA's of -0,15 and -0,25 respectively (Figure 14b). However, the forage estimates were very high for KTR, high for KTB and high for KRD, which does not explain why these habitat types should be avoided. In the Bonferroni analysis the KTR and cleared red turf savanna (KRD) were combined as they are essentially the same habitat type, the one being more open than the other. In the summer the COA for both KTR and KTB are approximately zero (Figure 14b), although the Bonferroni analysis shows that they are significantly (p < 0,05) avoided. As can be seen in Table 4 there is a very high ratio of DEC to INC grass species. A major portion of these DEC grass species, however, is *T. triandra* which is only really palatable when it has young shoots or in a post burn flush. The knobthorn turf savanna's are seldom burnt, and thus the grass components often had a lower forage potential than was expected on a species basis, and as a result of an inadequate fire regime were characterized by a dense woody component, which gives cover to predators. The palatability of the dominant grass species, lack of a burning regime and the cover afforded to predators are probably all factors that limit the use of this habitat type by buffalo.

During the hot, dry presummer there is intensive utilization of SSU and SSD by the buffalo, with 64,14% of the observations being made in this habitat type (Table

15). The COA was a high 0,5, although the biomass estimates were only 1956 kg/ha and 1764 kg/ha for SSU and SSD respectively (Table 4). The dominant palatable grass species in these habitats is *P. maximum*, and observations showed that buffalo intensively utilized these sandveld woodlands, were responsible for considerable biomass reduction and trampling and that the *P. maximum* growing in the shade of trees like bushwillows and round-leaved kiaat were greener due to the shading effect, and that the buffalo used to push their heads into multi-stemmed bushes to feed on these grasses.

The MTS was also shown to be positively selected for in the presummmer season (Table 18) with a COA of 1,75, and although this habitat type constituted a mere 5,62% or 738 ha (Table 3) of the study area, 9,82% of the buffalo observations for this season where made in this habitat type (Table 15). Biomass figures of 2105 kg/ha and 2197 kg/ha for MTS and MTD respectively were higher than those for the sandveld areas, but the reduced woody proportions meant a reduction in shade cover and hence the grass becoming dry and unpalatable earlier in the season than in the SSU.

The SSU and particularly MTS habitat types were characterized by high proportions of *Hyparrhenia filipendula* and *Themeda triandra* (see Chapter 2). In a study of palatability factors and nutritive values of the food of buffalo in Uganda, Field (1976) found a correlation between buffalo preferences and the percentage of green leaf of the above mentioned grasses. This association may be important in terms of habitat selection in the present study and contribute towards the reduction in movement patterns and home range in the summer months when the grass was green and most palatable.

In terms of the thicket communities, a marked seasonal pattern of winter utilization and presummer/summer rejection occurred. In the summer months the Bonferroni confidence intervals revealed a negative selection against RTW and RTH habitat types. During this period the biomass of these large riverine areas (19 % of study area - Table 3) ranged from very high (4530 kg/ha) for RTW to medium (1945 kg/ha) for RTH (Table 4). Although the RTW had a high proportion of palatable DEC grasses (66% - Table 4), the characteristically dense riverine vegetation of the summer months may not be suitable for a herd of buffalo to graze in. Risk of predation by lions in dense cover escalates and, therefore, these habitats are not really suitable for buffalo in the summer months.

As the winter months approached, many of the natural pans dried up, the buffalo began to range more extensively and the RTW habitat became an important food and water resource with positive selection of this habitat as determined by the Bonferonni confidence intervals (Table 17) and the COA (+0,19 - Figure 14c). The biomass in this habitat was still high (3986 kg/ha - Table 4) and water readily available in the Sand river. These factors, combined with a winter die back in riverine scrub and resulting better visibility are presumed to be responsible for this increased positive selection. The RTH community remained selected against, with medium to low forage availability (1909 kg/ha - Table 4).

Depletion of resources in the narrow RTW habitat towards the end of the winter necessitated that the buffalo moved away from this area in the presummer months, resulting in a selection in proportion to percentage occurrence in this season (Table 17).

The *Euclea* calc-brack thickets, whether undisturbed or cleared, offer low to very low forage and fuel potentials in all three seasons (Table 4). Biomass maximums of 1159 kg/ha were recorded in CBD in the summer months, with biomass dropping to 178 kg/ha in CBT in the winter months. The Bonferroni confidence intervals for the presummer and winter months (Table 17 and 18), reveal a utilization pattern in proportion to percentage occurrence, with negative selection in the summer months (Table 19). This pattern was also found in the COA analysis (Figure 14c). Therefore, although in terms of available forage the *Euclea* calc-brack thickets should not be selected for by buffalo, a pattern of utilization in proportion to percentage occurrence has emerged. The reasons for this are probably two fold: these areas were regularly visited in movement from one area of resources to the other and, therefore, although not used as grazing areas the buffalo were recorded moving through these areas; also due to the open nature, and subsequent good visibility in some of these areas, they were regularly used as resting areas.

DISTRIBUTION, MOVEMENT PATTERNS AND HOME RANGE

The herd was often found grazing in very much the same area as it was seen the day before, but subsequent analysis of the spoor showed that the herd walked quite some distance in the night, returning to the same area as the day before. It was, therefore, important to monitor the herd movements by following their tracks and plotting their route on a map in the field. Thus buffalo feed primarily in the early evening and very early morning in the SSW, and cover considerably more ground in search of food and water at night than consecutive daylight sightings of herds make evident (Table 21).

Particularly in the presummer months, the herds would select intensively for the area surrounding a particular watering point. This would result in the herd drinking at the same waterhole for up to eight days, and grazing in approximately the same woodland areas over this period. This led to a visible reduction in available biomass, which was followed by movement to another area. In the winter months the herds were more mobile, moving large distances at night, and grazing in a completely new area the following day (Figure 16b). These winter movements, at times, resulted in treks of over 10 km in a night, with the buffalo moving off again the following night (Table 21).

In the hot wet summer months the herd moved in a roughly rotational pattern between different feeding and resting grounds within the area of the home range being used (Figure 16a). These rotational patterns can be seen at two levels, the first is the roughly circular route the herd takes around its home range over the year cycle (Figure 16b), with the Sand river running west to east through this range. This pattern complemented the summer vs winter utilization of the home range (Figures 16a & 16b). Summer movements were restricted to the areas south of the Sand river, whereas, winter movements included regular movement across and along the area to the north of the Sand river. A general movement towards rivers and riverine vegetation in the winter months is in line with results elsewhere (Eltringham *et. al.* 1973, Sinclair 1977, Conybeare 1980).

At the second level, the movement patterns in the summer home range followed a roughly circular route, with certain areas being ignored, and others being regularly visited to graze in. The movements in the winter, however, did not show a regular pattern, the herd moved large distances in search of good grazing and then settled in these patches to graze. It also became apparent that selection for habitats and movement paths showed a seasonal tendency, factors such as water availability, grass biomass and grass quality played important roles. The movement patterns that the herd followed in their reduced summer home range, differed quite markedly from those used in the early and late winter months.

Plotting herd movements on a daily basis showed that the study herd seemed to have specific grazing areas or patches that it tended to prefer. Movement between these grazing areas often followed a similar route with certain favoured drinking sights being involved in these movements, and certain paths being used to move to these areas. Therefore, it may be possible to predict where the herd is likely to graze at a specific time, and to delineate specific grazing areas that are of importance to the herd, and may be important in terms of management.

During summer the minimum home range area was occupied, which corresponded with conditions of green vegetation and abundant surface water, with the NHR being 41,48 km^2 and an AIU measure of only 13,12 km^2 (Figure 15a). This coincided with the peak calving period in January/ February. These reduced movements, therefore, were probably the result of good grazing being available in localised areas and the reduced ability of the herd to move large distances as a group with very young calves. During the hot wet summer months strong selection was shown for mixed tree savanna (valley sides dominated by *Combretum* and *Acacia* trees), cleared and encroached contour seeplines and turf grasslands (after burning and rain). This was accompanied by the relatively small home range and intensive utilization of valley systems, seeplines and regular drinking points (Figure 16a). Movements from drinking to grazing patches followed well defined routes.

As the winter months approached the buffalo herd started to expand its home range, with extensive utilization of areas that where ignored in the summer months. The NHR increased by 290% to 120,94 km^2 with an AIU of 21,02 km^2 in 34 different clusters or nuclei (Figure 15b). This pattern of range expansion was accompanied by more intensive utilization of tributary woodlands, thickets and riverine areas for grazing and the areas to the north of the Sand river. An expansion in home range size is opposite to the results of Western (1975) who found that buffalo in the semi-arid Anboseli ecosystem showed a progressive contraction in home range in the dry season with concentration around water.

From the months July to September, the buffalo herd started to select the sandveld woodlands more intensively for grazing, usually utilizing a restricted grazing patch for a number of days. Movements to waterholes that still contained water, followed regular routes, and the herd was responsible for extensive trampling and grazing in the feeding patch. This was accompanied by a slight reduction in THR from 138,04 km^2 (winter) to 114,93 km^2 in the presummer months. The NHR, however, underwent a large (299%) reduction to 40,4 km², and an AIU of 20,01 km² (Figure 15c).

If one examines Figures 15a - 15b it is apparent that the clusters of AIU's are generally concentrated in the southwestern area of the home range, this area, therefore, comprising the core area of the home range of the study herd.

Leuthold (1972) reported a minimum density of 4,1 buffalo per km² in the Tsavo National Park. This density corresponded roughly to that found in the Tarangire area, Tanzania (Lamprey 1964), in a similar habitat. This is far less than that reported from the Queen Elizabeth National Park, Uganda, an area with a very different water regime (mean density = 15,6/km²; Field & Laws 1970).

In the eastern Transvaal there are much lower buffalo densities than those found in East Africa. The density of buffalo in the KNP is only 1,32/km², which is lower than that of the SSW which stood at 2,16/km² in 1991, assuming that the buffalo population utilize the majority of the available area within the two reserves. The mean size for herd No.1 was taken as 248, this corresponds to a minimum density of 2,07 buffalo per km². The bushveld habitat of the eastern Transvaal Lowveld and the relatively lower rainfall of this transition zone between arid and moist savanna biomes are probably important factors restricting southern African buffalo populations. The slightly higher average rainfall, less intensive culling programme and high percentage proportions of certain habitat types in the SSW are probably the main factors that are responsible for the higher buffalo density in the SSW compared to the KNP.

It has become apparent that the buffalo herd did show strong seasonal selection for home range and certain habitat and physiographic regions within these home ranges, that their movements were responsible for selecting the most suitable and not necessarily the best available habitats, and that they do not show a fixed pattern of range utilization, but rather alternate between three different patterns of range utilization, that correspond with the three seasons. The pattern of selecting different habitats at different times of year was also found by Vesey-Fitzgerald (1960) in the Rukwa Valley in southwestern Tanganika and Sinclair (1977) in the Serengeti.

DAILY ACTIVITY PATTERNS

Buffalo herds tended to show highly synchronized activity patterns with the majority of individuals engaged in the same activity at the same time. Social interactions, however, are not synchronized and are dependent on herd activity, sex, age and individual status.

The basic activity patterns of the western study herd were described quantitatively, while I looked for variations on a daily and seasonal basis. The daily programme or regime has been extensively covered and patterns pertaining to weather conditions, local food and water availability and seasonality have become apparent. Throughout the year there seem to be two grazing peaks on a daily basis (Figure 17a). However, the lengths and timing of this grazing activity vary on a seasonal basis, in accordance with the changes in ambient temperature. As can be seen in Figure 17a some level of grazing activity (10 - 15 %) is maintained through the late evening and very early morning. The peak in the first grazing period of the day occurs from 04h00 to 08h00 (Figure 17a). From 09h00 to 16h00 the majority (70 - 80 %) of the herd were found resting, usually in closely grouped bunches in the shade of trees (Figure 17b). During this period approximately 10 % of the herd were found to graze. By 17h00 the majority of the herd would be grazing, usually moving slowly in the direction of water. Grazing in summer usually continued until 21h00, after which the majority of the herd would be found resting or ruminating (Figure 17a & 17b).

As the winter months approached the nights became far colder, with the result that the majority (± 80 %) of the herd were found to be resting/ruminating by 19h00 and only beginning to graze at around 06h00 (Figure 17b). The result of this extended resting period, was that although the herd only began to graze at 07h00 this feeding period extended right through to 12h00, and even during the midday period (13h00 - 15h00) at least 30 % of the herd were found to continue to graze (Figure 17a). The second grazing peak of the day started at around 15h00 and was completed by 19h00 (Figure 17a) when the majority of the herd began to rest/ruminate until the following morning (Figure 17b). This pattern of predominantly feeding in daylight and resting for much of the night in the winter months was probably attributed to the fact that the temperature at night was low, but the days were mild which did not necessitate the herd resting in shade in the midday.

The buffalo were exposed to the height of food scarcity in the presummer months, when the days were hot, but rain had not yet fallen, thus the available forage was at its lowest. These reductions in biomass have been shown in Chapter 2. The result of these conditions on the grazing vs resting/ruminating pattern was an extended early morning grazing period from 04h00 to 11h00, with at least 20 % of the herd grazing through the midday period and another relatively long grazing period in the afternoon/ early evening from 16h00 to 22h00. On average 20 % of the herd continued to graze through the night (Figure 17a). The results of this on the resting/ruminating schedule was a short resting period from 23h00 to 03h00 at night and 12h00 to 15h00 in the midday (Figure 17b). As can be seen in Figure 17b only 50 - 60 % of the herd were to be found resting/ruminating in these periods, with the result that the herd became less closely bounded and spread out over a greater area. This could potentially increase the risk of predation by lions, and reports from the drought years 1983/84 showed that the herds did indeed fragment into smaller groups in the drought and that lion predation increased dramatically (see Chapter 6).

From the data presented it seems as if the buffalo herd under study spent more daylight hours grazing, although in summer and especially presummer some level of grazing was maintained through the night. This is in contrast to the study of Grimsdell & Field (1976) who found that buffalo in the Rwenzori National Park grazed more at night than at day. Leuthold (1972) also found that buffalo in Tsavo National Park feed primarily at night.

The study herd of buffalo in the SSW habitually drank twice a day with peaks in the early morning and late afternoon. As can be seen in Figure 17c there was not a great variation in the timing of the two times of day the herd went to drink. However, careful examination shows that in the hot wet summer months and the hot dry presummer months the herd drank early in the morning (05h00 - 07h00) and again in the early afternoon (15h00 - 17h00). It is presumed that drinking in the early afternoon helped to relieve the water and heat stress of midday. Whereas, in the cooler winter months the peak drinking periods were shifted to the midmorning (08h00 - 10h00) and early evening (17h00 - 19h00) (Figure 17c).

Data for a buffalo herd in the Rwenzori National Park are provided by Grimsdell & Field (1976) who found a mean grazing period of 8,9 h in the wet season and 9,5 h in the dry season with an average for both seasons of 9,1 h. They also studied the feeding habits of two tame female buffaloes whose over-all average grazing time was 5,7 h per day over a three month period. Grimsdell & Field (1976) studied buffalo in an area characterized by a bi-seasonal year and found little difference in the mean grazing period between the wet an dry seasons, although ruminating period in the wet season was half that in the dry season ($p < 0,01$).

The mean grazing period for the study herd of buffalo in the SSW was 10,6 h in the summer, 9,2 h in winter and 15,4 h in the presummer months, which for the summer and winter months is comparable to that found in East Africa. Therefore, the mean grazing period in summer and winter did not differ very much, although mean grazing period was lengthened in the presummer months at the hight of food scarcity.

The longer feeding time in the presummer did not necessarily mean that the buffalo ate more at this time, in fact they may well have eaten less, and in terms of nutritional value the food was certainly less adequate. The most likely reason for the difference was that during the dry hot presummer the vegetation was sparser and the buffalo had to spend more time looking for edible parts.

A second, but not alternative, explanation may be that more food has to be ingested in the dry season in order to extract an equivalent amount of nourishment from it. However this is unlikely. Dry food has a lower specific gravity than succulent material and, due to stratification in the rumen, the retention time is greater. Hence in the dry season, food remains in the rumen for longer periods than in the wet season, but becuase the capacity of the rumen is constant the amount eaten has to be reduced (Stanley Price 1977). The seasonal rumination period was reduced in the period winter to presummer (Figure 17b), and it can only be presumed that the buffalo had to spend the longer periods walking and looking for food in a grazing patch in this period.

An interesting observation at this time of year was that feeding buffalo regularly pushed their heads into clumps of bush and presumably found better quality grazing because of the shade and possible higher moisture levels in this microhabitat.

The scan samples have indirectly revealed an important finding with regards to feeding in late winter and presummer during which there was a marked increase in browsing activity by individuals from the herd (Table 20). This was especially apparent in closed *Combretum* woodlands, browsing being restricted to a few common woody species (Table 20). Although buffalo were recorded browsing on 418 occasions, this only represented 2,09% of the feeding observations. These observations were, however, concentrated in the presummer months when the veld was dry and there was lower available grass biomass. This increase in browsing under poor pasture conditions was also reported by Mloszewski (1983) in the dry season in parts of Zimbabwe's Gona-Re-

Zou National Park and by Sinclair (1977). These observations show that buffalo are largely grazers but are capable of eating a range of herbaceous species as well.

Looking at Figure 18a -18c it can be seen that there is an almost perfect inverse relationship between grazing and resting/ruminating behaviour. Winter was characterized by the herd being approximately 80 - 90 % synchronized in its activities except for midday when almost equal proportions of each activity pattern were evident (Figure 18a). In presummer the pattern was very similar, except that higher proportions were resting at midday (Figure 18b). In summer there was an almost perfect inverse relationship between the grazing and resting/ruminating activity (Figure 18c).

If one looks at the social interactions, it can be seen that in the winter and presummer months (Figure 19) the percentage of social interactions observed while conducting scan samples was in the region of 1 to 3 %. However, in the summer months social interactions were observed in up to 13 % of the scan samples. It, therefore, seems as if most of the social interactions, including sparring, courting, flehmen expression and mating were concentrated in the summer months. Furthermore, if one examines Figure 19 it becomes evident that the levels of social interactions were observed in two peaks, namely in the early morning and another small peak in the late afternoon/early evening. It, therefore, seems as if the herd under study concentrated their sparring for position in the dominance hierarchy and sexual interaction in the cooler daylight hours of the day in the summer months. This coincided with the peak in adult male numbers in the breeding herd through summer and peak mating activity in late summer.

CHAPTER 6: POPULATION DYNAMICS

INTRODUCTION

The present study was conducted in the SSW, the population of buffalo therein being a good model for the study of population growth trends. In the early 1980's the buffalo population underwent a drastic decline as a result of drought conditions. The population has subsequently recovered to its former numbers. Reasonably accurate records are available of annual counts of the buffalo population, the numbers of buffalo hunted with legal permits, the number of buffalo killed by predators, the number of buffalo that have died from disease, drought or other natural causes and the number of buffalo removed in game capture operations for live sale. The data have been used to analyse the trends in the population growth of buffalo in the SSW.

EFFECTS OF THE 1982/83 DROUGHT

Before the population crash that occurred in the buffalo population in 1983/84 the SSW buffalo population was relatively stable between 1100 and 1200 (Figure 20). However, the annual census in 1984 revealed a total count of around 460 buffalo (Figure 20). This represented a 60% decrease in the population from the previous year (Figure 20). Following this crash the population increased at an average of 12,3% per year. The result of this rate of increase is that the population has recovered to around its former numbers. As can be seen in Figure 21 herd 3 (the Mala Mala herd) increased at the highest rate, but with a decline from 1988 to 1989. The reason for this decrease, however, was that a proportion of this herd was captured and sold as live animals. Herds one and two have increased at around 12% per anum for the last eight years. The other herds (4, 5 and 6) have not been increasing at similar rates, and the fact that the herd size from the post drought periods were in the regions of 45 to 23 buffalo may have affected their rate of increase. It is also conceivable that sex ratios in these herds were not suitable for the similar rates of increase found in herds 1, 2 and 3.

REASONS FOR THE POPULATION CRASH

When the records of the warden were analysed it was possible to establish what the causes of death during the population crash were and to determine whether there was any seasonal pattern in this mortality. Figure 22 shows that the major factor responsible for death was predation by lions. It can also be seen that in the months January to July predation by lions was limited to around 14 animals per month. However, this figure increased to around 35 animals per month in the presummer months and, after the summer rains had failed, up to 45 animals in the month of October. This figure was down to twenty buffalo per month by the end of December, following midsummer rains (Figure 22).

Death due to malnutrition or dehydration occurred at low levels in September to November, but increased to 33 in December and 10 in January, following the failure of the early summer rains. No further deaths as a direct result of malnutrition/drought occurred in the drought period. A few buffalo were shot in the months March, June and October, but these numbers were so low that they did not influence the general decline associated with the drought (Figure 22). The deaths that occurred in the other category were due to such factors as early calf death, being stuck in mud, broken legs and infected wounds (Figure 22), and are not believed to be drought related.

As can be seen in Figure 23 the rainfall in 1982 was far below the longterm average at 193 mm, with rainfall in 1983 also far below at 487 mm. In subsequent years the rainfall has ocillated around the average (Figure 23). The numbers of buffalo that died per year are shown on the same figure. It can be seen that in 1982 fifty buffalo carcasses were found, and in 1983 this increased to 181 carcasses. In the following eight years from 1984 to 1991 this figure had declined to between 15 and 30 carcasses found per year. It, therefore, must be concluded that the lower than average rainfall (drought) of 1982/83 was the underlying factor responsible for the large decline in buffalo numbers seen from 1982 to 1984. This does not necessarily mean that all deaths were directly drought related, and the increase in lion predation on buffalo is believed to have had a major influence (Figure 22).

PREDATION IN THE LONGER TERM

The frequency and results of interactions between buffalo and predators were monitored. Lions are the most significant predators of buffalo in the SSW. Hyaena densities in the reserve are low and it is doubtful that they are responsible for many fatalities. Leopard densities are relatively high and a leopard was responsible for killing a newborn calf in April 1990. Predation by lions on individuals from the breeding herds does not occur often, predation being restricted to bachelor males.

Unfortunately records of the proportions of other game species killed by lions in the 1983/84 period are not available. However, when one examines the levels of predation by lions in some of the years from 1985 to 1990 (Figure 24) it is apparent that in 1985 7,8 % of the kills reported were of buffalo. This figure, however, was far lower in 1987 (1 %), 1989 (0 %) and 1990 (2 %). These figures lend further support to the theory that lion predation on buffalo increases in years when rainfall is far below average. Reports in the records show that in the 1983/84 period the buffalo herds became less stable with the large herd structure breaking down and smaller groups being established. It is conceivable that these smaller groups were more vulnerable to predation by lions because of a breakdown in the large group defence mechanism and a decline in body condition.

Looking at Figure 24 it can be seen that impala are the prey species most often reported as being preyed upon by lions, the levels varying from 23,6 % to 36 %. Wildebeest (13 % to 24 %) and zebra (14 % to 21 %) are the next most frequently reported prey species, with lower levels of predation on warthog, waterbuck, giraffe and buffalo. It, therefore, seems as if impala, wildebeest and zebra are the main prey base for lions in the SSW, with predation on buffalo increasing in drought years, provided the herd structure dissipates.

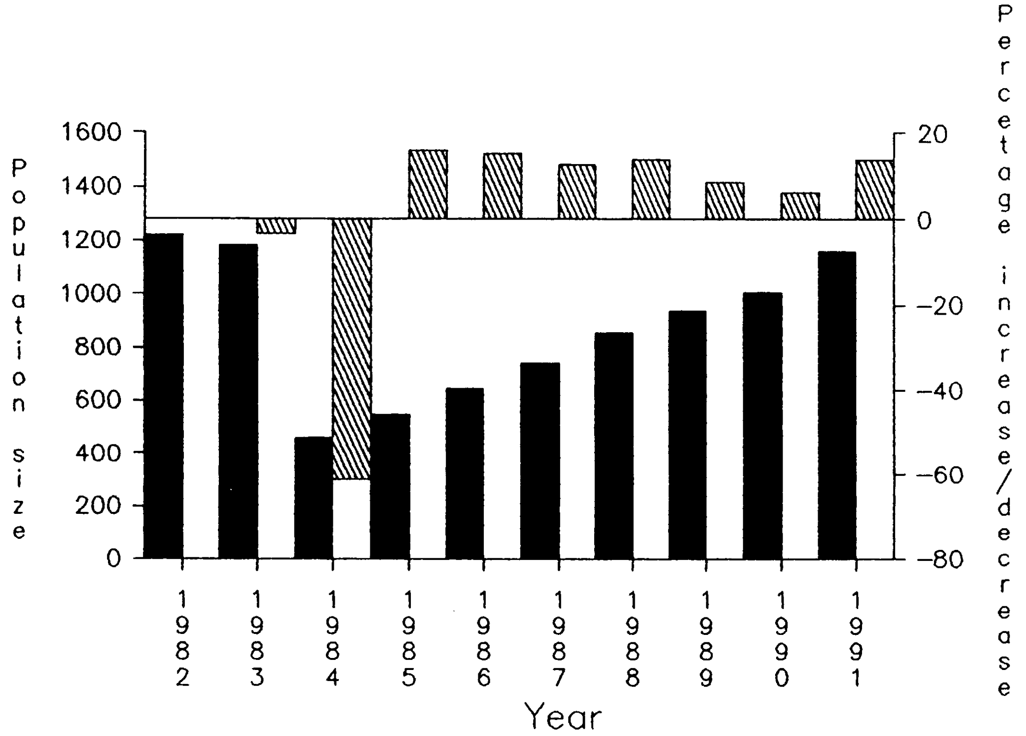


Figure 20. Bar chart showing the annual census total counts of buffalo from 1982 to 1991 and the percentage increase or decrease that the population showed from year to year.

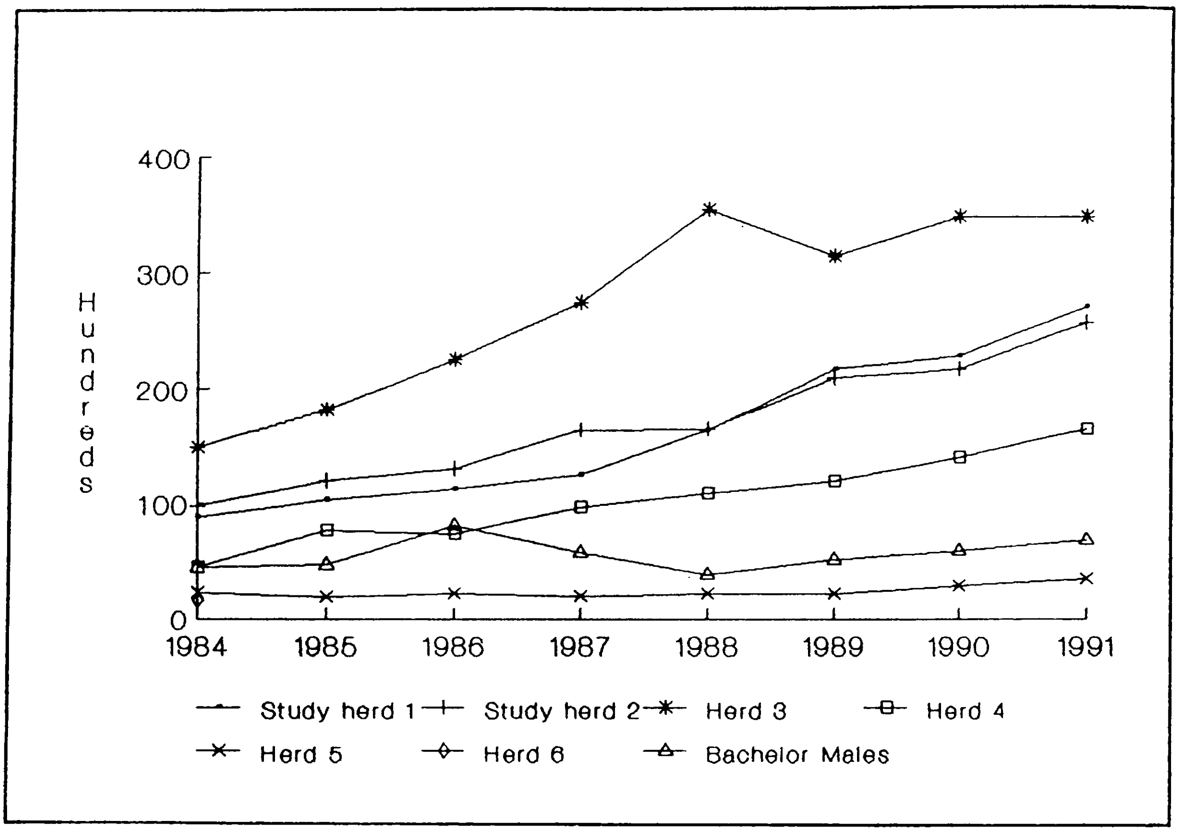


Figure 21. Diagram to show the increase in the size of each herd in the SSW from 1984 to 1991.

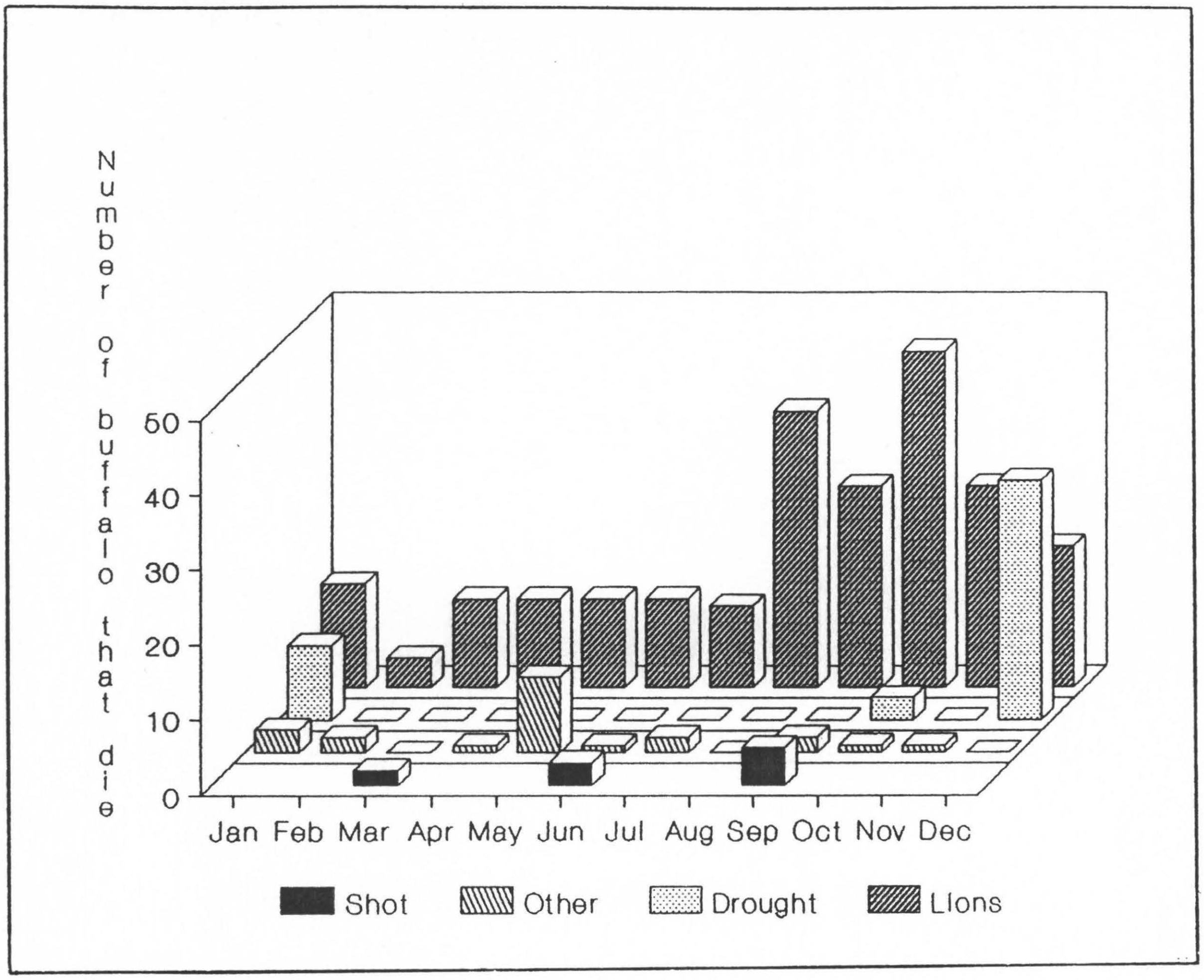


Figure 22. Diagram to show the numbers of buffalo that died per month in the drought period and which factors were directly responsible for these deaths.

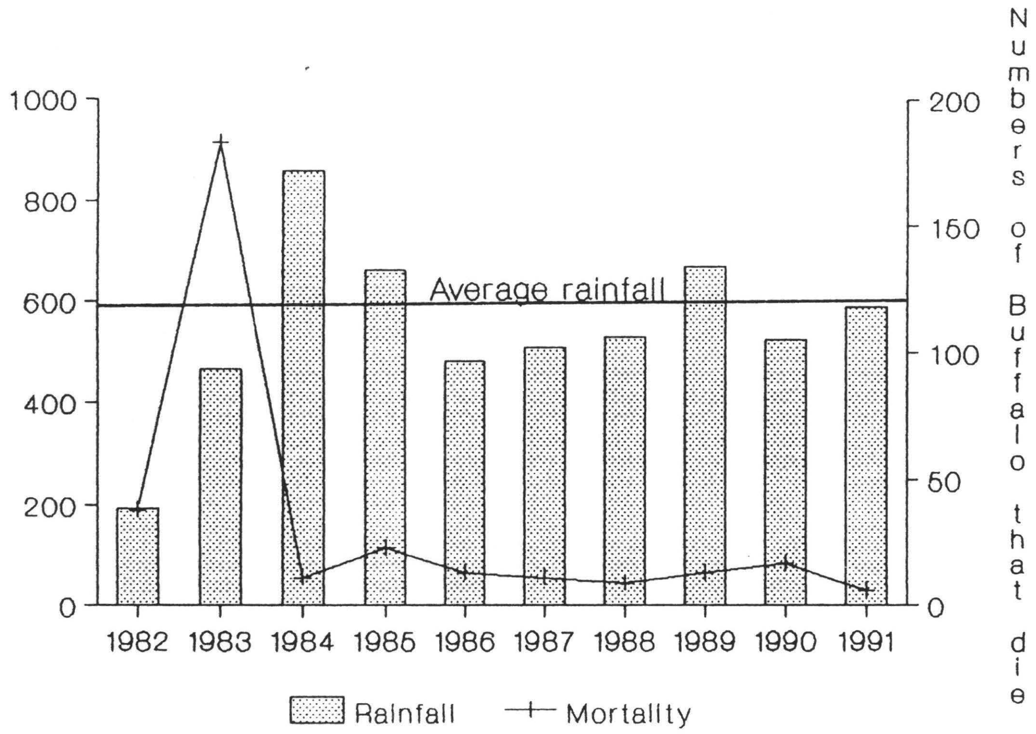


Figure 23. Diagram to show the annual rainfall figures and numbers of buffalo that died per anum from 1982 to 1991.

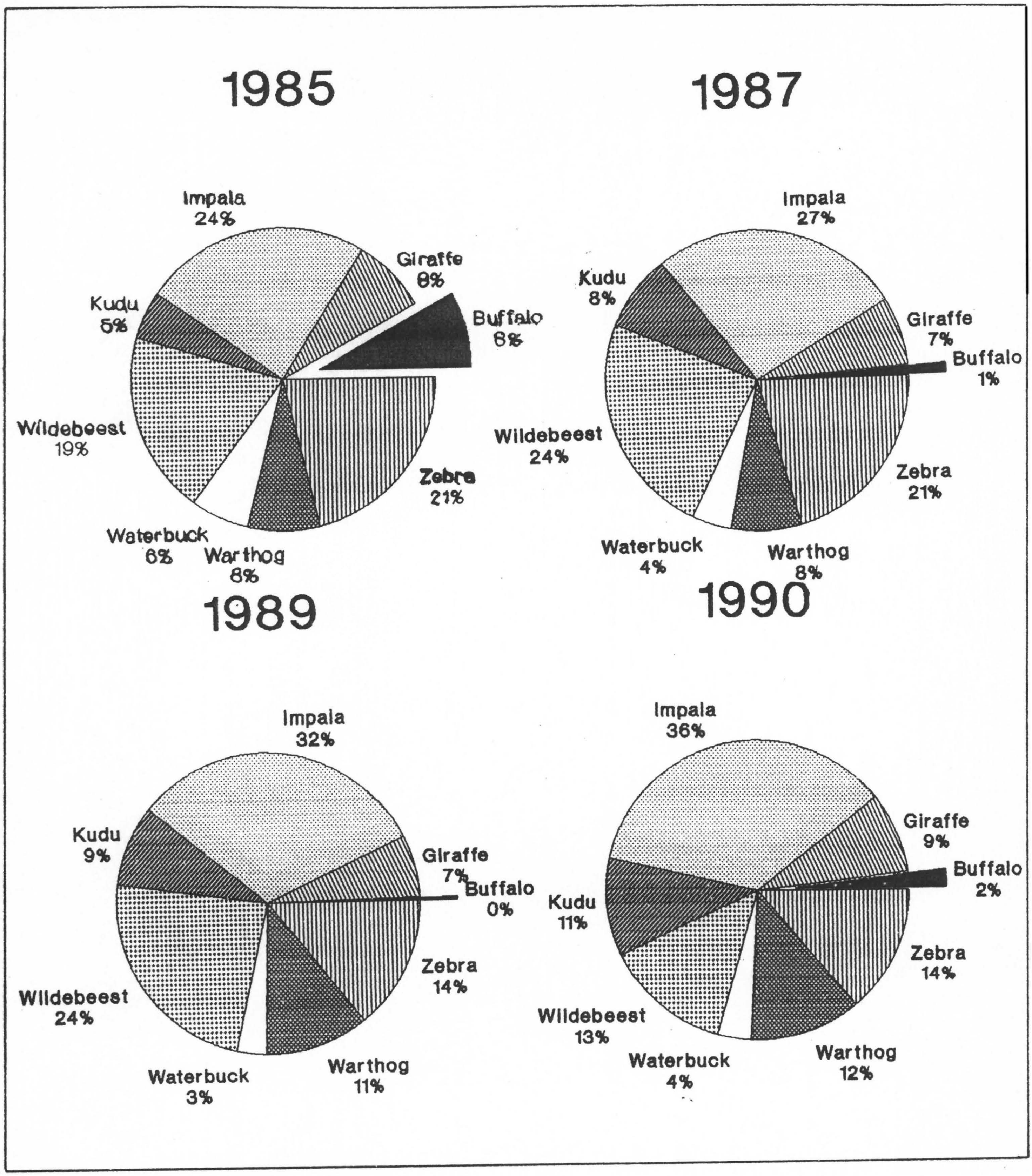


Figure 24. Pie charts to show the proportions of lion kills provided by each game species in 1985, 1987, 1989 and 1990.

CHAPTER 7: COMPARISON WITH THE ECOLOGY OF OTHER BUFFALO POPULATIONS AND CONSERVATION

Southern Africa, and especially the eastern Transvaal Lowveld is internationally famous for its wildlife and its conservation areas, perhaps even as renowned as the Masai ecosystem of East Africa. At the same time it is well known that its human population is growing at a very high rate. In the Lowveld the large Kruger National Park and other privately owned game reserves have been set aside for the purpose of nature conservation and for public enjoyment, and efforts are made to safeguard these areas. However, the growing human populations will necessarily lead to ever-increasing pressure on the land in general, and hence, on National Parks and especially privately owned land set aside for conservation.

It is hoped that the present study will provide some baseline data on the buffalo in the SSW, that is applicable in other conservation areas in the eastern Transvaal Lowveld. Moreover the results and subsequent discussion may be valuable, first in terms of the conservation and management of the buffalo in these systems and secondly in the development of utilization programs that complement the ecological and economic importance of the buffalo. It now remains to compare the results and conclusions reached in the present study with those found in other similar studies and formulate a theory on the control of movements by large mammalian herbivores.

Buffalo are known to occur in a wide range of habitats in Africa from dense lowland to montane forest, including a range of woodland and savanna biomes inbetween. It, therefore, seems reasonable to presume that habitat selection and home range patterns will vary according to biome type. This study was conducted in the south eastern Lowveld (Acocks 1975) which is typically a mixed woodland savanna ecosystem. In this discussion I will try to keep comparisons to studies with similar habitat types.

The savanna buffalo in the SSW are gregarious, occurring in herds of 250 - 350 animals which is similar to results obtained in other studies (Sinclair 1977, Whyte *et. al.* 1990).

Vesey-Fitzgerald (1974) in the Arusha National Park found that the size of grazing groups of buffalo varied on a seasonal basis, with large herds forming in the dry season and then fragmenting into smaller groups in the wet season. It is important to note, however, that there were virtually no predators in the park and this could have a very important role in herd formation. During the period of the present study, which took place during average rainfall years, the herd structure remained stable throughout, and risk of predation was always prevalent. The drought conditions of 1983/84 in the SSW were reported to induce a fragmenting of herd structure.

The basic social groups that buffalo form, the restriction of females to breeding herds, adult males forming bachelor groups, very old males being solitary, seasonal fluctuation in the size of bachelor groups and skewed sex ratios in the adult class have also been found in other studies (Grimsdell 1969, Mloszewski 1983, Prinns 1987, Sinclair 1977). However, in contrast to the studies of Kruger (1990) and Mloszewski (1983), herds in the SSW were not found to consist of subgroups with the herds occasionally splitting into smaller groups and then regrouping at a later stage.

The proportion of bachelor males in the reserve was 5,4% in 1990 and 5,8% in 1991, compared to 5,9% in the Sengwa Wildlife Research Area in Zimbabwe (Conybeare 1980), 6,9% in the KNP (Pienaar 1969) and 5,7% in Serengeti during the wet season (Sinclair 1977). As in the studies of Grimsdell (1969) and Sinclair (1977) the proportion of bachelor males increased in the dry season and as the rainy season started, they began moving back into the breeding herds.

Buffalo in the SSW showed significant differences in terms of habitat selection in the various seasons. The study by Sinclair (1977) also showed a pattern whereby buffalo selected different habitats at different times of year. From the results of the vegetation study it was possible to conclude that buffalo selected the most suitable habitats in the various seasons and that the most suitable habitat was not always the habitat with the highest available biomass. Available grass biomass does not seem to be the only factor controlling habitat selection in the buffalo in the SSW.

Home range sizes are smaller than the 200 - 250 km^2 reported by Conybeare (1980) in Zimbabwe, but are much larger than the 9,4 - 9,6 km^2 recorded at Rwenzori National Park with 1200 mm annual rainfall by Eltringham & Woodford (1973). Leuthold (1972) estimated the home range of a herd of 350 in Tsavo with 510 mm annual rainfall to be only 85 km^2 but this was only based on a few weeks observations and may be an under-estimate. These studies all dealt with total home range. The results presented in the present study show that although there is not much seasonal variation in total home range size, the normal home range estimates for the various seasons are quite different and show that home range estimates have to be analysed for internal structure.

In certain studies it has been found that buffalo tend to reduce their home range size in dry periods/seasons (Western 1975). This, however, was not found to occur in the SSW population and it is believed that the provision of many artificial water sources throughout the reserve (Figure 7) allows buffalo to range extensively in search of grazing and, therefore, they do not have to concentrate along the Sand river which was historically the perennial water base.

Buffalo densities in the SSW (2,16 per km^2) and 1,32 per km^2 (KNP) are the lowest reported in the literature. A slightly higher density of 2,8 per km^2 was reported in the Sengwa Wildlife Research Area in Zimbabwe (Conybeare 1980). Densities of 4,1 per km^2 in Tsavo (Leuthold) and 4,5 per km^2 in the Tarangire (Lamprey 1964) are also much higher, but still far lower than the 15,6 per km^2 reported in the Lake Manyara

National Park (Field & Laws 1970). It is believed that the lower annual rainfall in the eastern Transvaal Lowveld is the reason for the lower buffalo densities.

Conybeare (1980) found that for buffalo in the Sengwa Wildlife Research Area in Zimbabwe, diurnal movement was greater than nocturnal in all seasons. However in the SSW nocturnal movements were generally greater than those in the day.

It has previously been suggested that buffalo numbers can increase to the detriment of the environment. It seems more probable, however, if the habitat cannot support a certain population, that the animals will decrease in number and the course of succession will advance to another stage. In other words that environmental pressures will restrict the population increases rather than the reverse. If one is managing a large reserve that approaches a natural system this may be a valid argument, but in one that is definately not a natuaral system and were buffalo have a high commercial value, certain population management measures are inevitable.

From the facts presented thus far it seems as if there are a number of parameters that control buffalo herd movements in a typical eastern Transvaal Lowveld environment. In years of average rainfall buffalo will tend to have a reduced summer home range, which facilitates grazing in preferred habitats, when the favoured grass swards are lush and most nutrient rich. This is also the peak calving period and it is believed that buffalo evolved synchronised calving at the time of highest available resources to ensure a high calf survival rate. A pattern of range expansion accompanied with a shift in habitat selection will occur in winter months. However, it is believed that if artificial water sources are not provided, buffalo will tend to select for areas around natural perennial water sources (rivers), and thus have a restricted range away from the summer range. At the height of food scarcity in the hot, dry presummer months buffalo will select for areas not utilized in the other seasons, with intensive use of mixed woodland where shade induces the best available grazing, provided water is available in artificial sources. Should these water resources not be available they would rely on perennial water sources and walk large distances daily to patches of suitable grazing. Thus water resources and available grazing are the main factors controlling herd movement, with reduced herd mobility in the calving season and increased risk of predation in dense vegetation playing less important roles.

Herd structure is maintained throughout in years of average rainfall. In drought years, however, buffalo herds will occasionally become less stable and split into smaller subgroups. In years of very high rainfall home range size should become much reduced, with herds staying in the most suitable habitat as long as available forage is present.

SUMMARY

The aim of the present study was to investigate the spatial, temporal and social organization of buffalo and their feeding behaviour in the Sabi Sand Wildtuin environment. On completing this investigation a theory was formulated on the control of movements, with regards to home range and habitat selection, by large herd forming mammalian herbivores. Results obtained in East African buffaloes (*op cit*) were used in the formulation of the theory and were used as a comparitive source.

Fieldwork was carried out in the Sabi Sand Wildtuin, a 570 km^2 privately owned conservation area in the eastern Transvaal Lowveld, South Africa. The vegetation associated with the types of terrain were described in detail, a total of 17 habitat types being described. Veld condition estimates and seasonal biomass changes in the described habitat types were determined. These data, including climatic data, were used in the interpretation of the habitat selection and home range data.

Methods for determining sex and age in the field were refined and recognition of individuals within the herds helped in the sex and age structure and herd stability studies. Methods for counting herds of buffalo from the ground were developed and used in the population size study.

Females were always members of breeding herds, with animals less than five years invariably being so. Adult males were often members of temporary male groups with old males sometimes found in bachelor groups and very old males sometimes found as lone individuals. Sex ratios in the classes calves to subadults did not differ from the expected 1:1 ratio, but adult females outnumbered males. The breeding herd was not found to have subgroups or social units smaller than the herd and the herds were stable, fragmentation into smaller groups or joining of breeding herds was not recorded. Bachelor male groups were found to exist in the dry season, but in the wet season these

groups dissipated with the bulls returning to the breeding herds to mate.

The buffalo in the SSW did not show random utilization of the available habitat types in proportion to their percentage occurrence. It was also shown that buffalo in the SSW select for various different habitat types in the various seasons, and that these habitats are the most suitable at the times of year when they are selected for.

The buffalo were able to adjust their movement patterns in the various seasons to accommodate the various shifts in habitat selection and water availability that accompanied change from season to season. The buffalo showed relatively fixed movement routes at two different levels. In the summer movements were generally restricted to areas south of the Sand river, whereas, winter movements included regular movement across and to the areas to the north of the Sand river. There was a general movement towards rivers and riverine vegetation in the winter months. The presummer months were characterized by reduced movement in various patches of sandveld savanna. However, the buffalo did not show a fixed pattern of range utilization, but alternated between these three different patterns in the appropriate seasons.

The buffalo herd showed highly synchronized activity patterns with the majority of individuals engaged in the same activity. Throughout the year there were two grazing peaks in the early morning and late afternoon/early evening. However, the timing and duration of these grazing peaks varied seasonally. Diurnal grazing periods are longer than those at night, but nocturnal movements were generally further than those in the day. Grazing periods in summer and winter were similar, but were much longer in presummer at the height of food shortage. There was an appropriate reduction in resting/rumination periods in presummer due to the longer periods spent walking looking for food. There was an almost perfect inverse relationship between grazing and resting/ruminating period in all seasons.

A marked increase in browsing behaviour was recorded in the presummer months at the height of food scarcity. There was a large increase in social interactions in the summer months, associated with the male dominance hierarchy in early summer and mating in the late summer. Peaks in social interactions occurred in the early morning and to a lesser degree in the afternoon in the summer months.

The buffalo population crashed from over 1100 animals in 1982 to 460 in 1984 due to the drought. The population increased at an average of 12,3% per anum to its former numbers by 1990. Mortality in the drought period was predominantly due to increased predation by lions as well as directly from dehydration/starvation. Predation by lions in years of average rainfall was usually low, less than 3% of reported kills.

OPSOMMING

Die doelwit van hierdie studie was om die verspreiding, tydsbesteding en sosiale organisasie van buffels, asook hulle voedings-gewoontes in die Sabi Sand Wildtuin en omgewing te bepaal.

Met die voltooiing van die ondersoek, is 'n teorie oor die beheer van beweging, met betrekking tot loop-gebied en habitat seleksie deur groot trop-vormende herbivore geformuleer, waarvan die buffel as voorbeeld geneem is. Die uitslae van soortgelyke studies op buffels in Oos-Afrika is gebruik om die teorie te formuleer en het ook as 'n bron van vergelyking gedien.

Die Sabi Sand Wildtuin is as studieveld gebruik: dit is 'n privaat bewaringsgebied in die Oos-Transvaalse Laeveld, Suid-Afrika, en beslaan 570 km^2. Die spesifieke tipes plantegroei wat met die verskillende terreine geassosieer word, is volledig bespreek - 'n totaal van sewentien habitat tipes is beskryf. Veld toestand beramings en seisoenale biomassa- veranderinge in die behandelde habitat tipes is bepaal. Hierdie inligting, wat weerkundige data insluit, is in die interpretasie van habitat seleksie en loop-gebied data gebruik.

Metodes om geslags -en ouderdomsbepalings in die veld te doen is verbeter en die herkenning van individuele buffels in die trop het bygedra tot die studie van geslags -en ouderdomstruktuur en tropstabiliteit. Die buffels is te voet gevolg en getel om die bevolkingsgetalle te bepaal.

Buffelkoeie vorm altyd deel van die teeltroppe, sowel as alle ander individue jonger as vyf jaar oud. Volwasse bulle is dikwels deel van tydelike bul-groepe, terwyl ouerige bulle soms in vrygesel-groepe en baie ou bulle as alleenlopers opgemerk is. Geslags-verhoudinge in die klas kalfies tot sub-volwassenes het nie van die verwagte 1:1 verhouding veskil nie, maar volwasse koeie was in die meerderheid teenoor volwasse

bulle. Die teeltrop het nie uit kleiner sub-groepe of sosiale eenhede bestaan nie, en die trop was stabiel. Fragmentasie na kleiner groepe of die samesmelting van verskillende teeltroppe is nie aangeteken nie. Vrygesel-groepe is veral in die droeë seisoen opgemerk, maar in nat seisoene het die groepe opgebreek om weer deel te word van die teeltrop vir paring.

Gedurende al die seisoene het die buffels in die SSW nie toevallige benutting van die beskikbare habitat tipes in verhouding tot die persentasie voorkoms toegepas nie. Daar was bewyse dat dié buffels verskeie habitat tipes in die verskillende seisoene uitgesoek het, en dat die gekose habitats die mees gepaste was vir daardie spesifieke tye van die jaar.

Die buffels het hulle bewegingspatrone van seisoen tot seisoen aangepas om die verskuiwing in habitat seleksie en die beskikbaarheid van water te akkommodeer. Die buffels het relatief vasgestelde bewegingsroetes op drie vlakke getoon: gedurende die somer is beweging oor die algemeen beperk tot areas suid van die Sandrivier, terwyl beweging in die winter 'n gereelde trek oor die Sandrivier en na die dele noord daarvan insluit. 'n Algemene neiging om nader aan riviere en oewer-plantegroei te wei, is in wintermaande opgemerk. Die voor-somermaande is gekenmerk deur verminderde beweging in verskeie kolle sandveld-savanne. Die buffels het egter nie 'n vaste patroon in omgewingsbenutting getoon nie, maar die drie bewegingspatrone is gewysig in die toepaslike seisoene.

Die buffels het goed-gesinkroniseerde aktiwiteitspatrone getoon, met die meerderheid individue besig met dieselfde aktiwiteit. Regdeur die jaar was daar twee spits-weidingstye per dag naamlik vroeg soggens en laat middag/vroeg saans. Die tydsduur en tye van hierdie spits-weidingstyd het egter seisoenaal gevarieer. Daaglikse weidingsperiodes was langer as dié van snags, maar langer afstande is in die nag afgelê. Weidingsperiodes in die winter en somer was soortgelyk, maar was langer in die voor-somer wanneer voedingsbronne uitgeput is. Daar was 'n merkbare vermindering van rustyd/herkou periodes in die voor-somer as gevolg van die langer periodes waarin geloop en kos gesoek is. Al die seisoene toon 'n amper perfekte inverse verhouding tussen weidingstyd en rustyd/herkou periodes.

'n Merkbare toename in die vreet van jong lote en blare is aangeteken in die voor-somermaande wanneer voedseltekorte die ergste is. Daar was 'n groot toename in sosiale-interaksie in die somer maande, dit word geassosieer met die manlike dominansie-hiëragie in die vroeg-somer en paring in die laat-somer. Spitstye in sosiale interaksie is in die vroeë oggendure en in 'n mindere mate in die namiddag, gedurende somer maande, aangeteken.

As gevolg van die droogte het die buffelbevolking se getalle geval van 1100 diere in 1982 tot 460 in 1984. Die bevolking het weer gegroei teen 'n gemiddelde van 12,3% per jaar, tot die vorige getalle teen 1990 bereik is. Mortaliteit gedurende die droogte het hoofsaaklik as gevolg van verhoogde leeuvangste voorgekom en ook direk as gevolg van ontwatering/hongersnood. Gedurende jare met 'n gemiddelde reënval is buffelsterftes as gevolg van leeuvangste gewoonlik min, naamlik minder as 3% van alle aangemelde leeuvangste.

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