THE PRESENT ECOLOGICAL STATUS OF THE BLUE WILDEBEEST (*Connochaetes taurinus taurinus*, BURCHELL, 1823) IN THE CENTRAL DISTRICT OF THE KRUGER NATIONAL PARK

by

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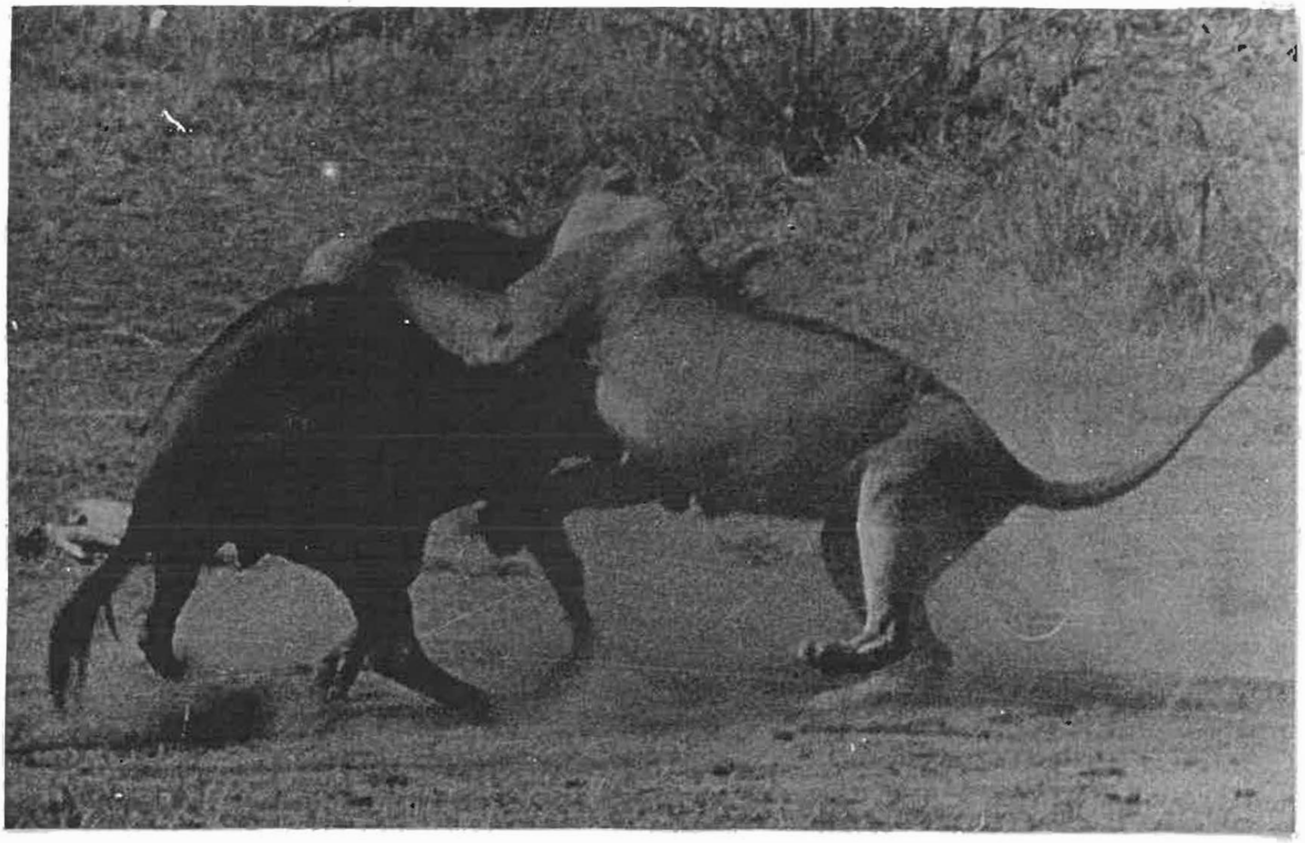

"You are so wild and beautiful and free
You live closer to the earth than man can ever be
Yet the hunter and the hunted live in harmony
You are so wild and beautiful and free.

You are so wild and beautiful and free
You've been living by your laws since this world came to be
If only you could pass some understanding on to me
You are so wild and beautiful and free."

John Edmond.

PREFACE

The research project described in this thesis was carried out in the Kruger National Park from January 1978 to November 1984 under the supervision of Professor John Hanks, Institute of Natural Resources, University of Natal, Pietermaritzburg.

These studies represent original work by the author and have not been submitted in any form to any other University. Where use was made of the work of others it has been duly acknowledged in the text.

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District Ranger Lynn van Rooyen and Senior Rangers (alphabetically) Messrs Kobus Botha, Ted Whitfield, Pat Wolff and Tom Yssel for allowing me free access to their respective sections during field work. Their trust is much appreciated. They are also thanked for assistance and enthusiastic interest in the project.

The late Philemon Chauke who was killed during field work. His friendship, company, cheerful assistance with field work and above all, his knowledge of the bush were sorely missed after his passing.

Messrs Don and Ross English and Wayne Vos - various assistants who enthusiastically continued with field work after the write-up phase of this project had started - who collected much useful data which would otherwise not have been available.

Messrs David Hughes and Bruce Aiken who, in spite of other interests, continued to supply information on marked lion prides and their kills. They are thanked for their contribution.

Dr Roy Bengis and his staff from the Veterinary Investigation Centre (Dept of Veterinary Services) for assistance with the capture of wildebeest and lions and for many reliable sightings of collared animals.

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ABSTRACT

Between 1969 and 1979 a dramatic decline occurred in the wildebeest (Connochaetes taurinus) population of the Central District of the Kruger National Park from around 14 000 to 4 700 (approximately 66%). Concern over this decline instigated this project whose broad objective was to determine the causes of the decline.

Lion (Panthera leo) and hyaena (Crocuta crocuta) culling campaigns were initiated in late 1974 in an attempt to alleviate predator pressure on the wildebeest population and ground counts to monitor the sex and age structure of the wildebeest population were initiated in 1978 to assess the effect that these campaigns were having on the population. These ground counts, conducted quarterly, were a main aspect of the field work of this project. Results showed that calf and yearling mortality, measured as a ratio of calves/yearlings per 100 cows, varied considerably from year to year.

As quarterly counts progressed a gradual distortion in the adult sex ratio became evident. The ratio declined from 2,5 cows per bull in 1978 to around 1,7 in 1980 but then returned to the original ratio by 1983. This distortion could not be related to sex-specific mortality.

Results from these counts showed that predator culling was not achieving its objective as it was conducted on too small a scale. Increasing the scale of the campaign was unacceptable so culling was terminated.

The second main aspect of the field work was a radio-telemetry study of lions which attempted to assess their impact on the wildebeest population. Sample sizes of lion kills proved too small for satisfactory analysis but the tentative conclusion drawn was that lions were potentially able to remove up to 85% of one years' recruitment.

Wildebeest population and sub-population trends were monitored from aerial census totals. These showed that 70% of the total decline occurred in only one sub-population whose summer grazing grounds were excised and its migration routes severed by boundary fences. Declines in other sub-populations were ascribed to changes in habitat condition induced by above-average rainfall cycles.

Overall conclusions were that fencing was mainly responsible for the decline; that the wildebeest population fluctuates in accordance with climatic cycles; and that lions are potentially capable of reducing the wildebeest population under unfavourable habitat conditions.

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CHAPTER 1

INTRODUCTION

1.1 GENERAL

The results presented in this dissertation form part of longer-term research and monitoring programmes which have been conducted on the blue wildebeest Connochaetes taurinus (Burchell, 1823) population of the Central District (hereafter referred to as CD) of the Kruger National Park (hereafter referred to as the KNP), since a persisting population decline in the area aroused increasing concern from 1969 onwards (Braack, 1973; Joubert, Pienaar, van Wyk & Smuts, 1974; Smuts 1975b; 1976b; 1978b). This decline as well as the various pertinent aspects of wildebeest ecology which have received attention from other workers in the CD will be discussed in the following chapter on population history. Results presented here are from the period between January 1978 when I received responsibility for monitoring the population dynamics of the wildebeest population, with the further objective of trying to determine the causes of the decline, and November 1984 when field work for the purposes of this dissertation was terminated.

1.2 EVOLUTION AND DISTRIBUTION OF THE GENUS CONNOCHAETES

1.2.1 Evolution and taxonomy

Wildebeest are considered to have evolved from a bovid stock of African origin whose appearance can be traced back to the early Miocene and appear to have evolved in their present day form during the Pleistocene (Wells, 1965 and Cooke, 1972 in Berry 1980a). They then became distributed across Africa during the radical climatic changes of the Quaternary period (Bigalke, 1972).

Wildebeest were (and still are) widely distributed in Central and Southern Africa (Berry, 1980a; Dorst & Dandelot, 1970; Smithers, 1983). Ansell (1972) discussed their past and present distribution and concluded that their general range had not altered significantly within historical times and recognised five sub-species. These are:

a) Cookson's wildebeest _C. t. cooksoni_ Blaine, 1914. From the Luangwa Valley to the Eastern Province plateau, Zambia.

b) _C. t. johnstoni_ Sclater, 1896. From Mocambique north of the Zambezi, southern Tanzania and southern Malawi (where now extinct).

c) Eastern white-bearded wildebeest _C. t. albojubatus_ Thomas, 1892. North-eastern Tanzania and southern Kenya east of the Rift Valley extending west to the Wembere plains.

d) Western white-bearded wildebeest _C. t. mearnsi_ Heller, 1913. Northeastern Tanzania and southern Kenya west of the Rift Valley including the Serengeti plains.

e) Blue wildebeest _C. t. taurinus_ (Burchell, 1823). The nominate sub-species which was described from a specimen obtained by Burchell in the north-western Cape Province in 1823 (Ellerman, Morrison-Scott & Hayman, 1953). This sub-species ranges west and south of the Zambezi River and beyond the Zambezi into south-western Zambia (Ansell, 1972).

The wildebeest populations of the KNP are therefore of the nominate subspecies C. t. taurinus, and are the only representatives of the genus Connochaetes in the KNP. The only other member of the genus C. gnou, whose distribution is restricted to the southern African subregion, is nevertheless confined to the central plateau of southern Africa and is therefore absent from the eastern Transvaal Lowveld and the KNP (Smithers, 1983).

1.2.2. Early history of the wildebeest population of the KNP

There is no fossil evidence of the occurrence of wildebeest in the KNP probably due to the lack of fossil bearing deposits but Plug (1984; in litt.) has evidence of their existence here from faunal remains at archaeological sites dated at ± 450 A.D. This is the earliest date for which there is positive evidence of their occurrence in this area, but it seems probable from Bigalke (1972) that wildebeest appeared in the Lowveld at some time during the Quaternary.

Du Plessis (1969), in his work on the past and present distribution of the Perissodactyla and Artiodactyla, lists several references for blue wildebeest but the oldest of these for this area was a record by Louis Trigardt for the Sand River in 1837 (in Le Roux, 1966).

There is very little on record to provide any indication as to the past abundance of wildebeest in the KNP area, but from the books and notes of the early white hunters it would seem that they had been numerous during the nineteenth century but were severely decimated by hunting before the proclamation of the Sabie Game Reserve in 1898 and the arrival of the first Warden Lt. Colonel James Stevenson-Hamilton in 1902. Kirby (1896), who favoured the area now encompassed in the CD of the KNP for hunting, had the following to say of wildebeest in the area ".... as their hides have considerable marketable value for converting into the best "riems", and they show good sport to a mounted man, they are probably greater victims to the rifle than any other of the larger antelopes. But for the astonishing numbers in which they existed a few years ago, they must long ere this have become extinct, few animals being more sought after by the itinerant hide hunter than these".

Stevenson-Hamilton (1929) attributes the survival of the larger antelope species in the KNP before its proclamation as a National Park to the presence of the tsetse fly (Glossina morsitans) which prevented the hunters from taking their wagons and horses into the "fly belts" which resulted in a less effective form of hunting on foot.

In 1896 came the rinderpest which severely depleted all of the susceptible game species in the area. Although wildebeest are susceptible to rinderpest (Plowright & McCullogh, 1967; Sinclair, 1979; Taylor & Watson, 1967), there is nothing on record to indicate the impact that this disease may have had on the wildebeest populations of the KNP, though Stevenson-Hamilton (1939a) states that the Bovidae with hairy rhinaria (including wildebeest) seemed to have been little, if at all affected by the disease. After the passing of the rinderpest it was discovered that the tsetse fly, to which the game had owed its survival, had disappeared completely (Stevenson-Hamilton, 1939a) and has not returned to this day.

This sudden "safe" access to previously infested areas should have led to another period of extermination by hunters but due to a general unawareness of the fact that the tsetse had disappeared and the disruption caused by the Anglo-Boer war, this did not happen and hunting continued at a rather reduced rate (Stevenson-Hamilton, 1929). This was the prevailing state of affairs when Stevenson-Hamilton arrived in the area in 1902.

The area between the Sabie and Olifants Rivers which included the present area of the CD, had by then been surveyed into farms which were owned by various "land companies" who had little use for the land at that time. As this area was considered to have a better potential for a game reserve than the Sabi Game Reserve itself, its administration as part of the game reserve fell under Stevenson-Hamilton in 1903 and under the National Parks Board of Trustees in 1926 and has remained so ever since.

The initial dearth of game is illustrated by remarks made by Stevenson-Hamilton (1937) who said of a tour made through the KNP in 1902. "Game was found only here and there. (Some areas) ... later to become so thickly covered with wildebeest that they looked like mobs of cattle scattered everywhere, then held but a few reedbuck and duiker".

1.3 OBJECTIVES OF THE STUDY

As will become apparent in Chapters 3 and 4, the trends in the wildebeest population of the CD were briefly as follows. From the few survivors of the depredations of the previous years, the population built up steadily after the proclamation of the KNP in 1902 for approximately the next 70 years. This build-up was interrupted by occasional periods of decline, but between 1970 and 1979 a dramatic period of decline amounting to a population "crash" occurred. Concern over this decline instigated this project and, while the broad objective was to determine the reasons for the decline and assess the present ecological status of this population, the project was conducted according to the following more specific objectives.

(i) To monitor the movement patterns of the various sub-populations by means of resightings of marked individuals. This was in order to substantiate the theory that sub-populations do occur in the population of the CD (Smuts, 1972; Braack, 1973) so that sub-population data could be confidently used to compare trends either in growth rates or structure of the three sub-populations.

(ii) To trace the history of the three sub-populations. This was to test the hypothesis that the major decline in the population occurred in the Western Boundary sub-population due to the erection of the game proof fences which cut across their traditional migration routes and denied them access to their major summer grazing grounds.

(iii) To continue to monitor sex and age structure of the population by means of ground counts for possible correlations with population and/or sub-population growth or decline and also with prevailing climatic conditions.

(iv) To assess the impact of lions on the wildebeest population by means of radio telemetry collars fitted to lions to assist in the location of their kills.

CHAPTER 2

THE STUDY AREA

2.1 GENERAL

The KNP lies along the eastern and northeastern borders of the Transvaal province of the Republic of South Africa (RSA) (Figure 2.1.1). The eastern boundary, which also comprises the international boundary between the RSA and Mocambique, lies along the Lebombo Mountains which are prominent in the the south but disappear completely in the north. The northern and southern boundaries follow the courses of the Limpopo and Crocodile Rivers respectively. The western boundary follows no natural features except in the extreme south where the Sigaas River constitutes the boundary, a small section north of the Letaba River where it follows the course of the Klein Letaba River and also in the far north where it follows the Levubu River for some distance.

The KNP is fenced along its entire periphery. These fences are not entirely "game-proof" as individuals of certain species manage to get through, under or to break them, but they have certainly curtailed all major movements of animals in or out of the KNP. The effects of these fences are discussed later.

In its entirety the KNP is situated in the area generally known as the "Lowveld" - i.e. the low-lying area below and to the east of the Drakensberg range and covers an area of some 19 400km². It lies between the latitudes 22° 20' and 25° 32' S and the longitudes 30° 53' and 32° 02' E. The highest lying land (approximately 835 m) is found near Malelane in the relatively mountainous southwest with a gradual decline to the east to relatively lower lying country varying between 180 m and 240 m above sea level.

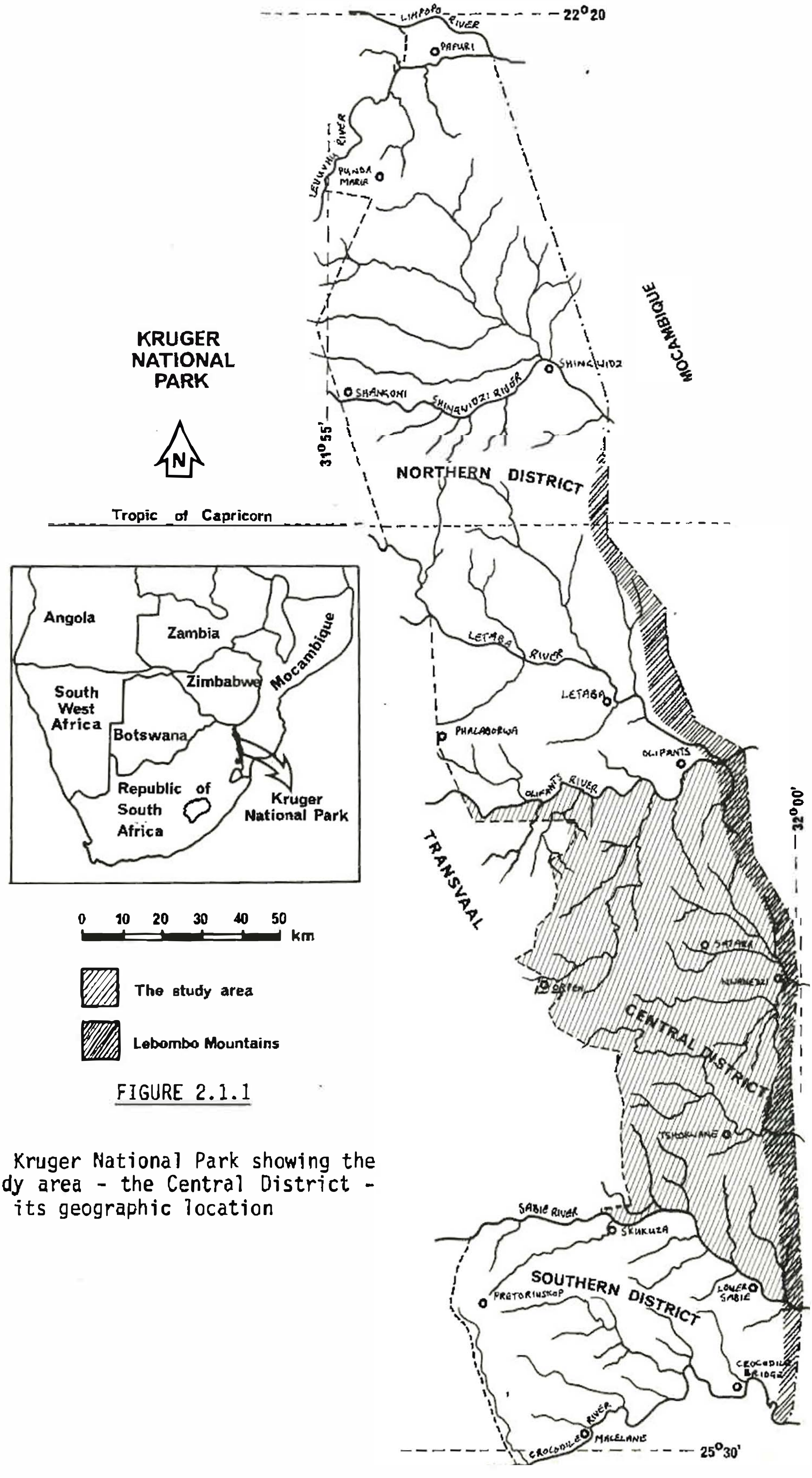


FIGURE 2.1.1

The Kruger National Park showing the study area - the Central District - and its geographic location

For administrative purposes the KNP is divided into three districts (see Figure 2.1.1): the Northern District which comprises the whole area north of the Olifants River, the CD (Figure 2.1.2) which has as boundaries the Olifants River in the north and the Sabie River in the south, and the Southern District which lies between the Sabie and Crocodile Rivers. Both the Sabie and Olifants Rivers are perennial and form fairly stringent faunal barriers which prevent any major movement by wildebeest out of the CD and thus, being contained also by fences in east and west, these wildebeest are considered here to be a discrete population. Although wildebeest also occur in the Northern and Southern Districts this study was confined to the CD and unless otherwise stated all further information, results and discussion pertain to this District only. This is the most important District as far as the KNP's wildebeest are concerned as it covers an area of only 5 517 km² or 28,4% of the total area of the KNP while the most recent population estimate for the wildebeest of the CD in 1984 was 8 026 which was 67,3% of the KNP's total population.

2.2 CLIMATE

In the KNP the majority of the rainfall occurs in the form of thunder-showers which are occasionally accompanied by hail. Rainfall is also experienced in the form of gentle "mist-rain" which may last for several days, or occasionally as very heavy downpours as a result of cyclonic conditions which move inland off the Indian Ocean and the Mocambique Channel. Most of this rainfall occurs during the summer months (Figure 2.2.1) between October and March. From rainfall data for the CD stations Tshokwane, Satara, Kingfisherspruit and Nwanedzi given by Gertenbach (1980a) it was calculated that 85,5% of the rain falls during these months.

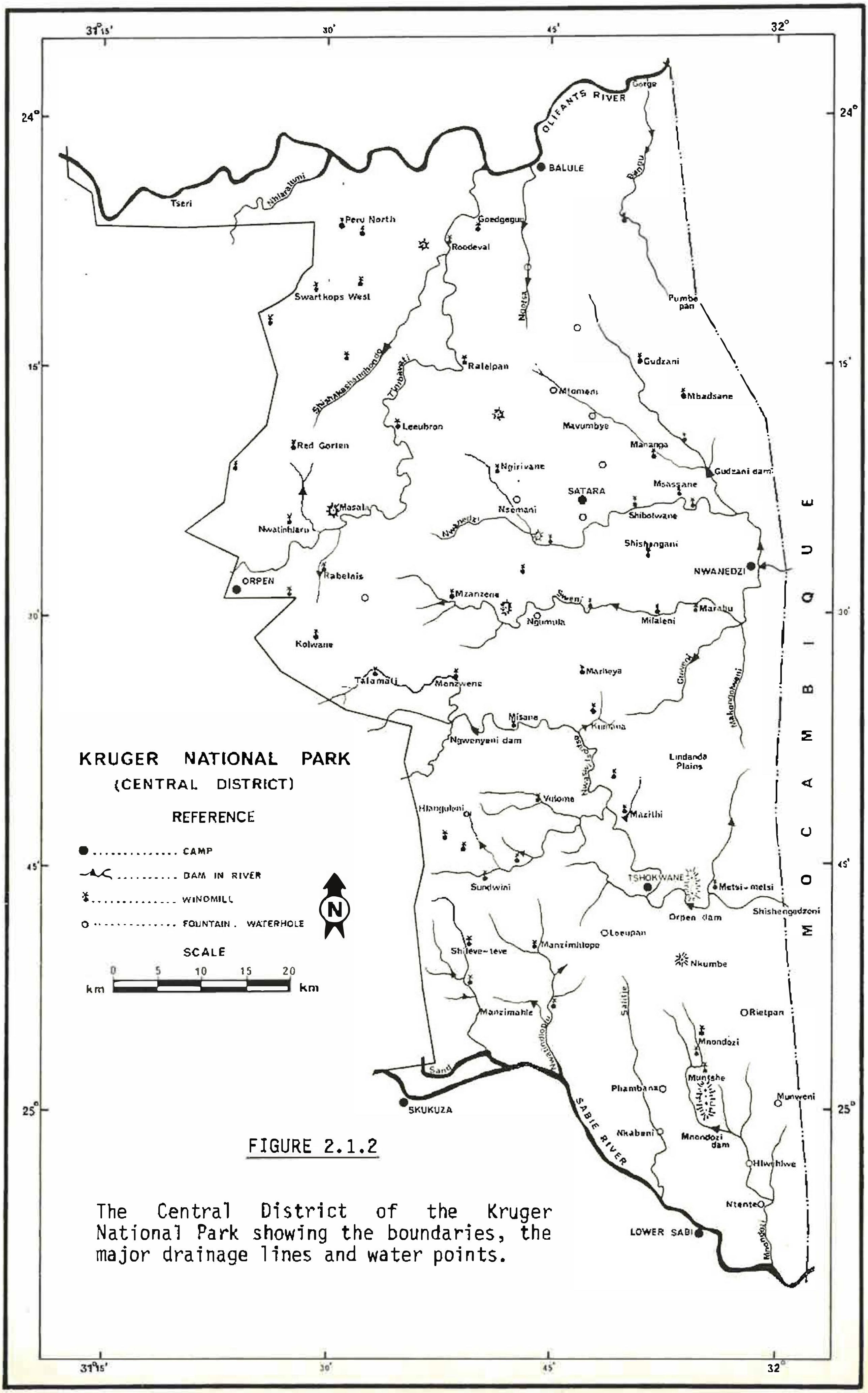


FIGURE 2.1.2

The Central District of the Kruger National Park showing the boundaries, the major drainage lines and water points.

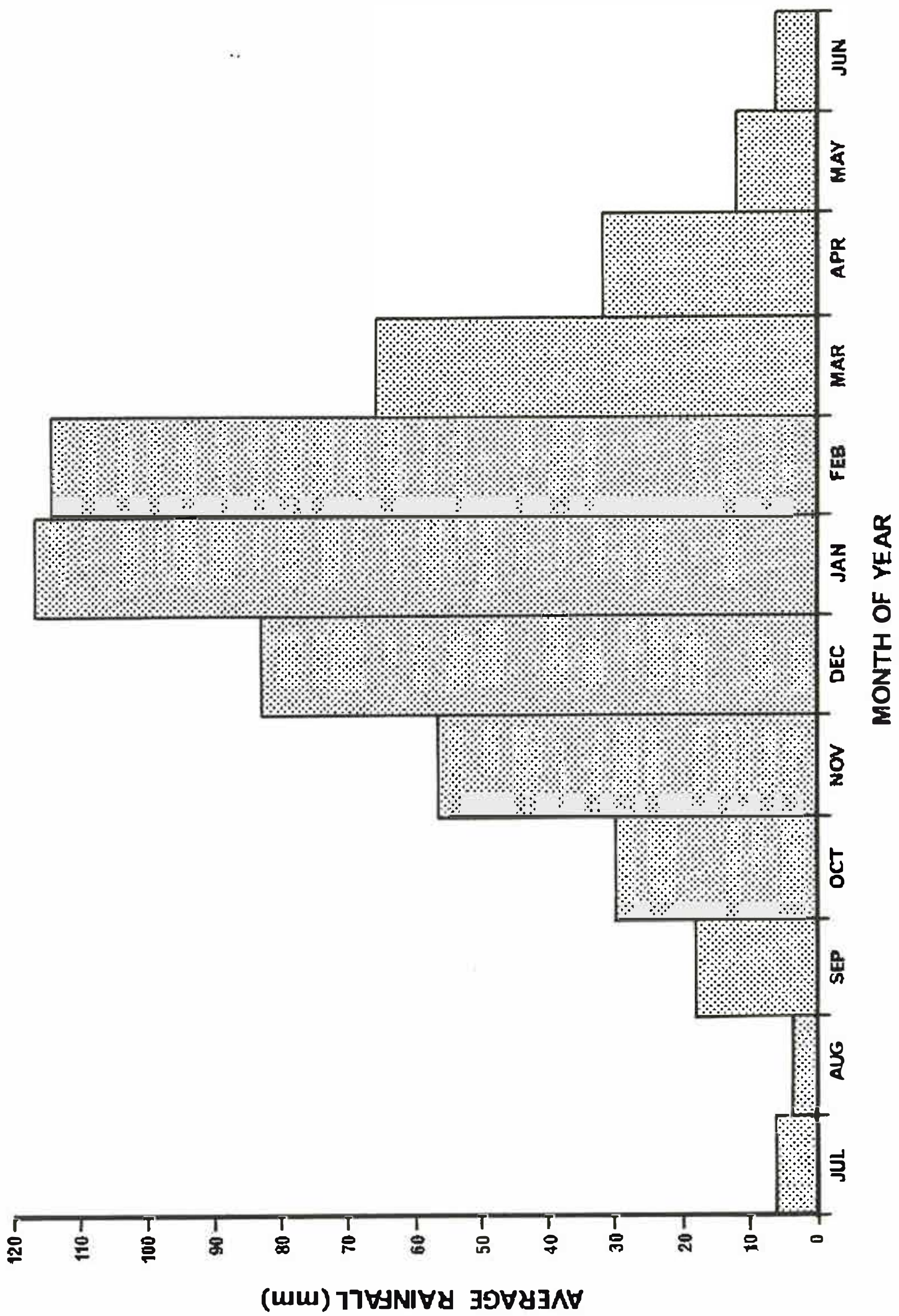


FIGURE 2.2.1: Average rainfall for respective months in the Central District of the Kruger National Park from pooled data from the stations Satara (47 years), Tshokwane (44 years), Kingfisherspruit (23 years) and Nwanedzi (14 years).

In general, precipitation decreases from south to north probably as a function of increasing distance from the sea and also increases from east to west due to increasing altitude. Thus the low-lying flat areas in the middle and north of the KNP have the lowest mean annual rainfall while the high-lying areas around Pretoriuskop in the south and Punda Maria in the north are relatively wetter. Gertenbach (1980a) compiled a rainfall map (Figure 2.2.2), from which it is evident that rainfall patterns in the CD do not differ greatly and vary between 500-600 mm per annum.

Of further interest from the data collated by Gertenbach (1980a), is the emergence of a pattern of wetter and drier rainfall cycles. According to Dyer (1975, 1976), Dyer and Tyson (1977) and Tyson and Dyer (1975, 1978) there is a quasi 20 year rainfall oscillation in the summer rainfall areas of RSA which consists of respective 10 year periods of above and below average rainfall. Gertenbach (1980a) found that the KNP cycle conformed to a large degree to those described by the above authors (Figure 2.2.3). The effects of these oscillations on wildebeest habitat and thus also on the wildebeest populations is discussed elsewhere in this thesis.

Generally, temperatures vary from 0°C to 40°C though occasionally temperatures beyond these extremes have been recorded. Temperature data from Skukuza, on the boundary of the CD, and Satara are given below.

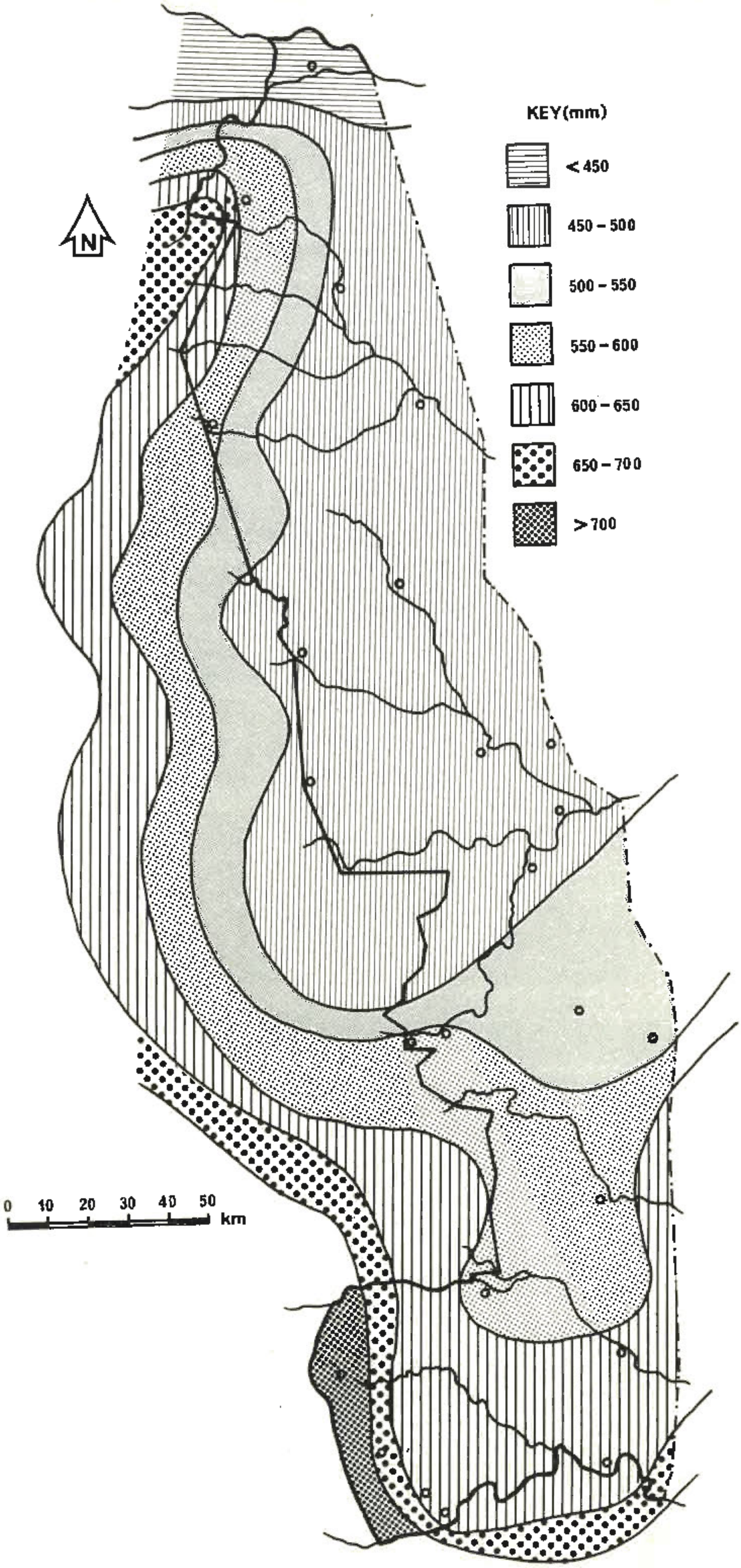


FIGURE 2.2.2: A rainfall map of the Kruger National Park (after Gertenbach, 1980a).

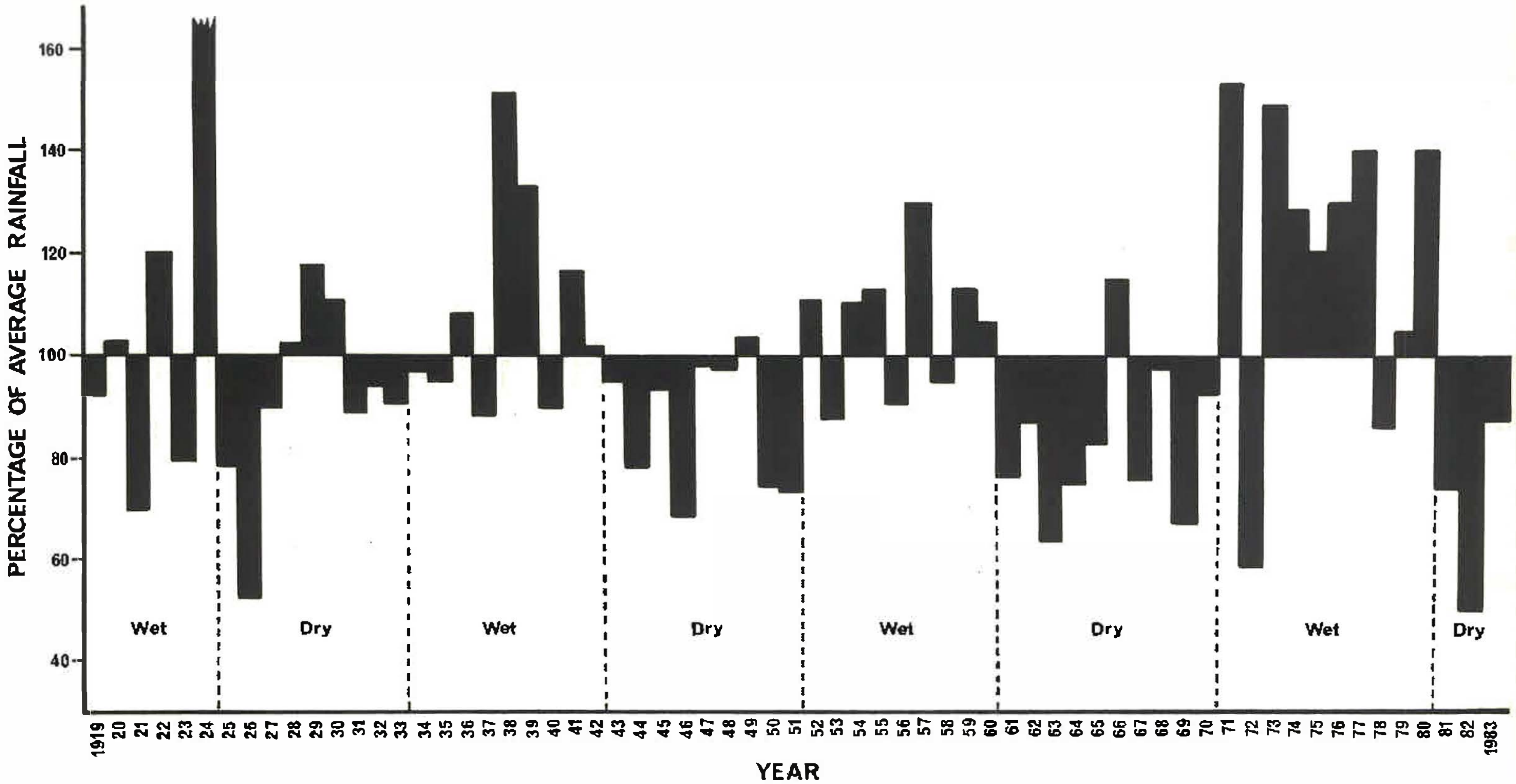


FIGURE 2.2.3: Annual rainfall shown as a percentage of the average annual rainfall from 1919 to 1983 in the Kruger National Park. Wet and dry cycles are highlighted. Respective years indicate the year in which respective summers began (from Gertenbach, 1980a).

Table 2.1.1: Various temperature (°C) parameters from Skukuza and Satara which may be considered representative of most areas in the Central District

PARAMETER	SKUKUZA	SATARA
Highest average monthly maximum	32,3 (January)	33,6 (February)
Absolute maximum	44,5 (November)	41,6 (January)
Lowest average monthly minimum	5,6 (July)	8,9 (June)
Absolute minimum	-2,5 (July)	8,0 (June)

Although the highest absolute maximum was recorded in November, the hottest months are December, January and February, while the coldest months are June and July. Temperature inversions are distinct in the more undulating landscapes (Gertenbach, 1983a) and this can result in the occurrence of frost in the low-lying areas on cloudless nights (Smuts, 1972).

Summers (October to March) are generally hot and humid while the winters (April to September) are cool and dry and relative percentage humidity may vary between 100% and less than 10% (Young, 1970).

At 25°S, photoperiod varies between 14 hours and 11 hours at the summer and winter solstices (Sadleir, 1969).

2.3 GEOLOGY AND SOILS

From various scources (Dept. of Mines, 1970; Hamilton & Cooke, 1965; Harmse, 1978; Houghton, 1969; King, 1963, 1978; MacVicar, 1973; Mountain, 1968; Schutte, 1974a & b; van der Schijff, 1957), Coetzee (1983) and Gertenbach (in prep.) have compiled concise accounts of the geological and geomorphological history of the KNP.

Some of this is of relevance to this study as the CD has been structured geologically, geomorphologically and thus also botanically into compartments which have separated the wildebeest population into partially discrete sub-populations. The relevant aspects of these accounts have been summarised here.

Almost all of the western half of the CD consists of Archaean granite and gneiss (Figure 2.3.1) which has given rise to a gently undulating landscape. In the southern granites the landscape has a typical and recurrent pattern of deep sandy summits each surrounded by a "seepline" fringe and intersected by clayey valley bottoms. In this undulating terrain, clay and sodium released from the weathering granite accumulates in the valley bottoms leaving leached sandy soils on the crests and clayey, sometimes sodic duplex soils (often with a massive prismacutanic structure in the underground horizons) in the bottomlands (Coetzee, 1983; Gertenbach, 1983a). On the middle slopes the hard impenetrable B horizon forces internal drainage water to the surface causing seasonal seepages. Along these seepages, belts of open grassveld develop (known as seeplines) which are the major wildebeest habitats in this area. In the northern granites, however, the occurrence of amphibolite is extensive and this has an important influence on the soils in that they tend to be more clayey. The uplands are less sandy and the seepline is usually absent, while the soil becomes increasingly clayey towards valley bottoms. The absence of the seepline renders the vegetation less suitable as a habitat for wildebeest.

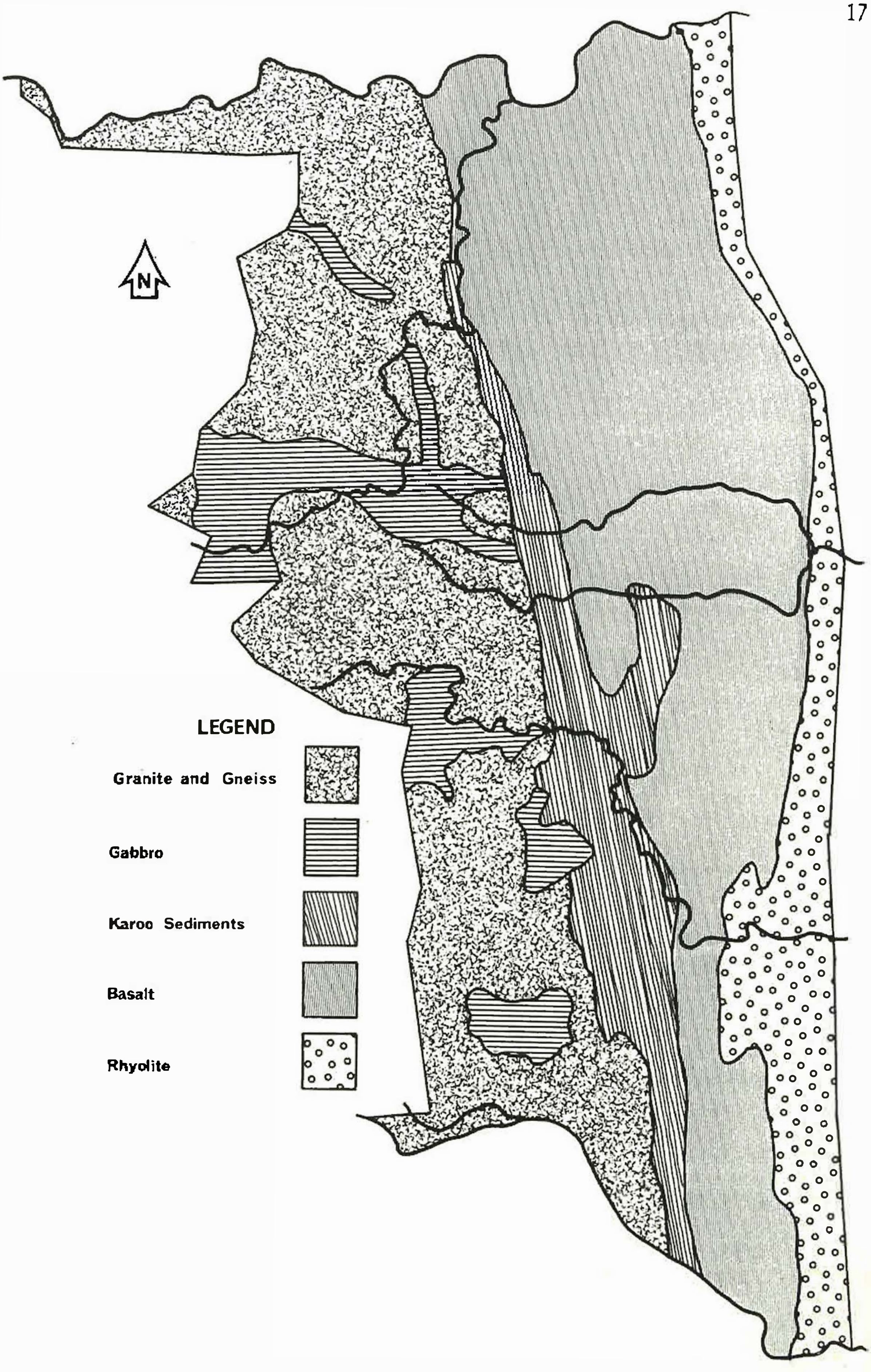


FIGURE 2.3.1: A simplified geological map of the Central District of the Kruger National Park

The western granites are interrupted by large gabbro intrusions. The soils that develop from gabbro are usually dark in colour and clayey and in the study area they form flat clayey plains or a gently undulating landscape with occasional hills and ridges. These gabbro intrusions with their flat clayey plains, constitute important habitats for wildebeest. The large central intrusion shown in Fig 2.3.1 extends to the west of the KNP's boundary into the Timbavati Private Nature Reserve (Joubert, 1983a) and forms part of the "Wildtuingang" (Brandt, 1948), an area of great importance to the KNP's migratory herds until it was fenced off.

The Karoo sediments occur as a long and narrow continuous zone down the centre of the CD. These sediments separate the granites in the west from the basalts in the east. These sediments include shale, mudstone, sandstone, grit, marl and coal (Coetzee, 1983) and throughout their length they support a dense plant community which is almost impenetrable to plains-loving wildebeest. These sediments separate the western and eastern sub-populations of the CD.

To the east of the Karoo sediments the basalts are to be found. They form an almost flat landscape and in fact are generally referred to as the "Lebombo Flats". It is on these basalts that the major concentrations of wildebeest are to be found. Two sub-populations occur which are basically separated by the rather flat watershed between the Sweni and Nwanedzi Rivers. The terrain is flat to mildly undulating, giving rise to landscapes which are generally open providing some of the best habitats for wildebeest in the KNP.

Finally to the east of the basalts are the rhyolitic Lebombo Mountains which rise above the adjacent basaltic plains as a result of their superior resistance to erosion. These rhyolites also dip towards the east, and eastern slopes tend to be more gentle than those facing west, and the nature of the terrain and its vegetation render it unsuitable as a major wildebeest habitat.

2.4 DRAINAGE AND WATER

The rivers of the KNP drain from west to east. In the CD the drainage lines are all tributaries of two major sub-systems - the Olifants River which ultimately feeds the Limpopo System and the Sabie River which forms part of the Incomati System (Pienaar, 1978). Of all the rivers in the CD, only the Olifants and Sabie are perennial and in the past few years even these have almost ceased to flow due to the increased demand for agricultural and industrial water upstream of the KNP and the droughts of the past few years. The other water-courses are all seasonal, flowing only when rainfall has been sufficient to allow some run off, but most retain some water in permanent or semi-permanent pools once the flow ceases (see Figure 2.1.2).

In order to obtain a more even distribution of water in the dry seasons, much effort has been put into providing artificial watering points. In the CD 34 dams with earthen and sometimes concrete walls have been built and 100 windmills with concrete reservoirs and drinking troughs have been sunk at 71 sites. The dams are well dispersed and now very few of the larger tributaries are without some form of water impoundment. These in conjunction with 16 troughs which are supplied with water from the Olifants River/Satara Rest camp pipeline make a total of 121 artificial watering points in the CD. Young (1970) studied the ecology of water in the KNP.

2.5 VEGETATION

Botanical work in the KNP was pioneered by van der Schijff in the form of his ecological study of the KNP's flora (van der Schijff, 1957) and also in his 4 000 specimen plant collection which still forms the core of the KNP's herbarium at Skukuza (Coetzee, 1983). Many aspects of the vegetation have subsequently received research attention and Coetzee (1983) includes a comprehensive survey of the resulting literature which need not be duplicated here. The KNP's research staff have recognised the importance of vegetation monitoring for which an essential pre-requisite is to map and describe the total species composition of the plant communities. This called for a semi-detailed vegetation classification system and four such surveys have been completed using the Braun-Blanquet technique (Gertenbach, 1978, in prep; van Rooyen, 1978; Coetzee, 1983).

The size and distribution of these plant communities render the mosaic so complex that it is impossible to chart them on maps of a convenient scale or to use them as practical management units. A coarser system was therefore required and Joubert (1975) proposed a new zonation. However, more recent studies of the abiotic components - climate (Gertenbach, 1980a), geology (Schutte, 1982; Schutte and Clubley-Armstrong, 1982), and soils (Fraser, 1983; Venter, 1981; Webber, 1979) have facilitated the development of the "Landscape" concept. Landscapes are identifiable by their plant communities and are large enough to serve as management units. Bell (1981) also adopts a "landscape" approach in a management plan for Kasungu National Park in Malawi. Coetzee (1983) defines a landscape as "an area with a recurrent pattern of plant communities with their associated fauna and abiotic habitat" while Gertenbach (1983a) uses "a landscape is an area with a specific geomorphology, macroclimate, soil and vegetation pattern and associated fauna". On this basis Gertenbach (1983a) identified 35 landscapes within the KNP of which 17 are represented in the CD (Figure 2.5.1). The following summarised descriptions and map are from Gertenbach (1983a), and include a note on their importance to wildebeest. A detailed listing of plants common to or characteristic of these landscapes was extracted from Gertenbach (1983a) and is given in Appendix A. Landscapes favoured by wildebeest are highlighted in this appendix and thus plants of potential importance in wildebeest habitats are indicated.

2.5.1 Olifants River Rugged Veld

In this strongly undulating terrain the dryness of the area is accentuated by steep slopes and shallow soils and as a result the vegetation shows xerophytic characteristics. The field layer is very sparse and never develops a stable grass cover even where grazing is very light or absent and seldom develops further than the pioneer stage. Because of the sparsity of the field layer fires are rare and as a result the woody component, which is largely dominated by Combretum apiculatum, Colophospermum mopane and Terminalia prunioides, can be quite dense, though seldom higher than five metres. As a result of the aridness of this strongly undulating terrain, the sparsity of the field layer and the density of the woody component, this landscape is not well suited to wildebeest.

2.5.2. Colophospermum mopane Shrubveld on Basalt

In the CD this landscape is represented only by its southernmost tip which extends across the Olifants River. It is absolutely dominated by Colophospermum mopane shrubs and as a result is of no consequence to wildebeest.

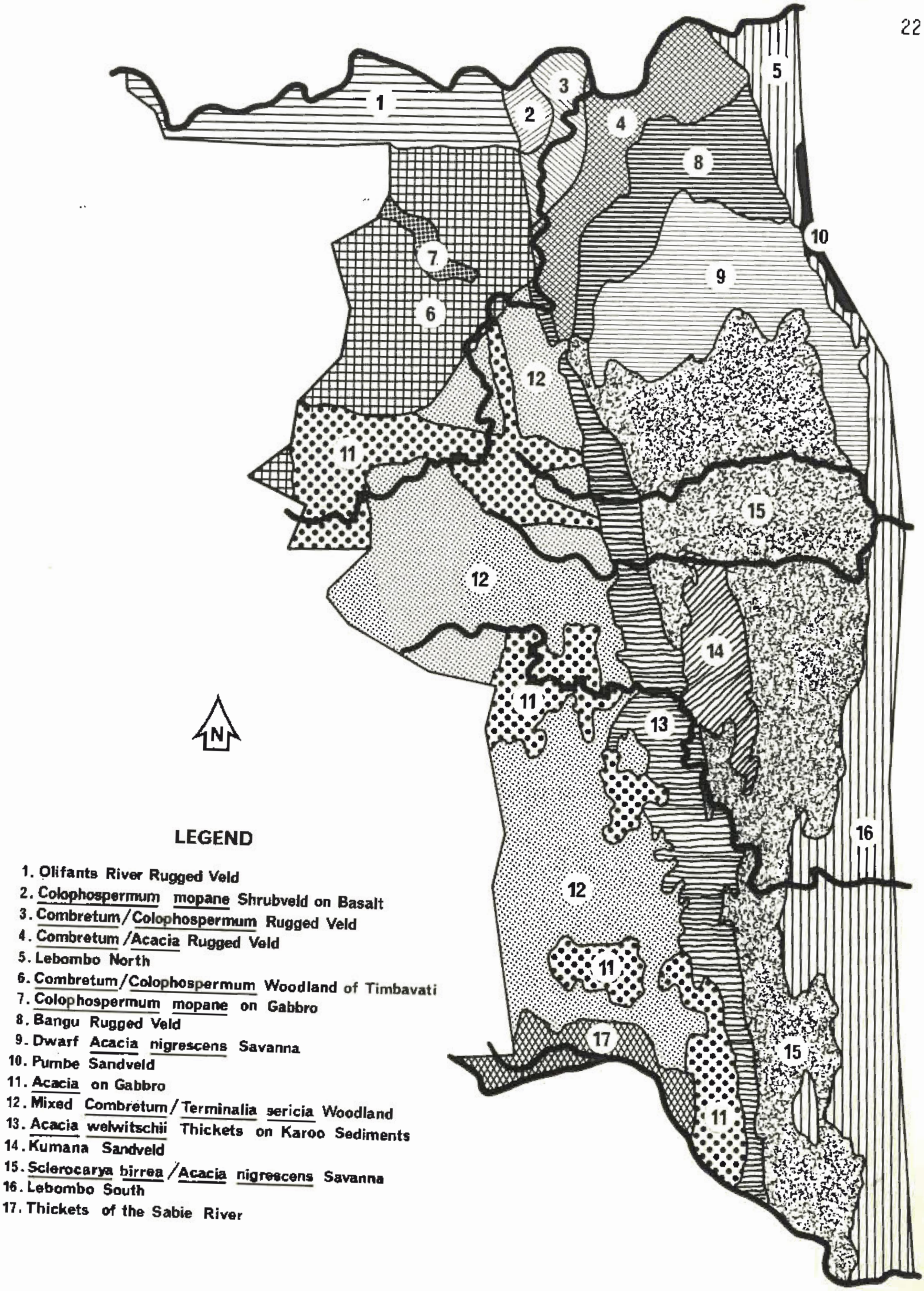


FIGURE 2.5.1: The landscapes of the Central District of the Kruger National Park (from Gertenbach, 1983a).

2.5.3. Combretum/Colophospermum Rugged Veld

This landscape is characterised by flat plains with rhyolitic outcrops. It represents only a small proportion of the CD. It is also dominated by Colophospermum mopane shrubs interspersed with Combretum apiculatum and Terminalia prunioides and thus also represents unsuitable habitat for wildebeest.

2.5.4. Combretum/Acacia Rugged Veld

The soils of this landscape are shallow and rocky outcrops and ridges are common. The climate is relatively arid and the field layer of the undulating middleslopes is therefore sparse to absent but is dominated by annuals such as Aristida congesta subsp. barbicollis, Enneapogon cenchroides and Urochloa mosambicensis. Forbs are relatively plentiful. The tree layer is dominated by Combretum apiculatum, Acacia nigrescens and Terminalia prunioides. Sesamothamnus lugardii which is typical of arid areas is also present in this landscape.

Along the river banks the grass layer is largely dominated by Panicum maximum and Cynodon dactylon. Phragmites australis is present on the sand in the riverbeds. The river banks are characterised by the relatively open tree veld.

Wildebeest numbers are relatively low in this landscape probably as a result of the denser woody component.

2.5.5. Lebombo North

This landscape is also only marginally represented in the CD. Soils are shallow and very rocky and up to 80% of the surface can be covered by stones and rocks. Thus the field layer is very sparse. In the north the vegetation is completely dominated by the tree *Androstachys johnsonii* and this, as well as the rugged nature of the terrain render the habitat unsuitable for wildebeest.

2.5.6 Combretum/Colophospermum Woodland of Timbavati

Although the sub-stratum of this landscape is mainly granitic, amphibiolite occurs extensively throughout and as a result the soils in certain catenas are relatively clayey and there is some evidence that the occurrence of *Colophospermum mopane* can be correlated with the presence of weathered products of amphibiolite in the soil (Gertenbach, 1983a). On the sandy uplands *Terminalia sericea/Combretum apiculatum* communities occur but as the soil becomes more clayey towards the bottomlands *C. apiculatum* becomes less dominant while *C. mopane* becomes more dominant.

The field layer is here also dominated by annuals, the most important of which, for both uplands and bottomlands, are *Pogonarthria squarrosa, Eragrostis rigidior, Aristida congesta* subsp. *barbicollis, Digitaria eriantha* var. *pentzii.*

As in the previous landscapes, the density of the woody vegetation precludes its use by wildebeest.

2.5.7. Colophospermum Mopane Shrubveld on Gabbro

This landscape forms a narrow intermittent strip intruding into the previous landscape and is also only marginally represented in the CD. In the Northern District it occurs more extensively. Soils contain relatively large amounts of clay. There are very few large trees in this shrubveld and there is once again an absolute dominance by mopane which renders it unsuitable as a wildebeest habitat.

2.5.8 Bangu Rugged Veld

This landscape stretches across the eastern basalts in a narrow strip from the Timbavati River to the Lebombo Mountains. Owing to the low rainfall and also to the shallow stony soils the area is relatively arid. The steep slopes and shallow soils cause the area to be erosion prone.

The vegetation of this area is described by Coetzee (1983) as an Acacia nigrescens/Grewia bicolor-dominated shrub veld. The area was severely overgrazed in the past and shows distinct signs of retrogressive succession. Apart from Acacia nigrescens and Grewia bicolor the following woody plants are also common: Terminalia prunioides, Acacia exuvialis, A tortilis, and, Dichrostachys cinerea subsp. africana. The field layer is sparse to moderate and the grasses are mostly annual species with a great variety of forbs present.

This shrub veld habitat is well suited to wildebeest and zebra and it was these two species that were mainly responsible for the overgrazed condition of this area in the past (Gertenbach, 1983a).

2.5.9 Dwarf Acacia nigrescens Savanna

This area is reasonably flat to concave with high lying plains. Soils are clayey in upland sites and are increasingly more so in valley bottoms where they may also be vertic.

The vegetation of this landscape varies from a pure grass veld on the vertisols to a stunted Acacia nigrescens savanna on the middle-slopes. Where pure grass veld occurs on the uplands it is dominated by Themeda triandra, Bothriochloa radicans, Digitaria eriantha var. pentzii, Panicum coloratum, P. maximum, and Enneapogon cenchroides.

On slopes where the soil is less clayey, woody plants occur more commonly and a dense low tree savanna dominated by Acacia nigrescens is characteristic. These small trees have a single stem and are usually between two and four metres high. The stunted growth form of the trees can be attributed to slow growth as a result of high moisture retention in the soil, combined with the high grass cover and regular occurrence of hot fires.

A unique component of this landscape is stands of Acacia borleae which occur on the brackish vertisols. The dense stands are approximately one to two metres high and almost impenetrable.

Dwarf A. nigrescens savanna is generally dense and consequently wildebeest occur only in low numbers.

2.5.10 Pumbe Sandveld

Only a small portion of this landscape extends into the KNP. It is a moderate to high shrub savanna with a moderate grass cover. It occurs to the east of the Lebombo Mountains, making it almost inaccessible and this, as well as its small area and shrubby character, render it most unsuitable for wildebeest.

2.5.11 Acacia Veld on Gabbro

The KNP's Gabbro intrusion extends from Malelane in the south to the Phonda Hills to the west of Shingwedzi in the Northern District. This landscape occurs in a series of "islands" of which a number occur in the CD.

In certain areas of the landscape the vegetation is dominated by stands of *Acacia nigrescens* trees which vary in height from three to seven metres, but where these knobthorn trees become more dense, the trees are usually lower. Otherwise the landscape is characterised by an open savanna with a dense grass cover.

Gertenbach (1978) divided the vegetation on gabbro, in the vicinity of Orpen, into two communities viz. *Chloris virgata/Acacia nigrescens*-shrubveld and the *Sclerocarya birrea/Acacia nigrescens* savanna. The first mentioned community occurs on shallow soil and normally has a sparser grass cover and is grazed more intensively. It is a low tree veld to a shrub veld with *Acacia nigrescens, Ziziphus mucronata,* and *Acacia tortilis,* as the most important woody species while

Chloris virgata, Cenchrus ciliaris, Sporobolus nitens, Enneapogon cenchroides, Schmidtia pappophoroides, and Digitaria eriantha var. pentzii are some of the dominant grasses. Forbs are common.

The Sclerocarya birrea/Acacia nigrescens-savanna occurs on deeper soils and has a dense grass cover that is not as intensively grazed. It is an open tree savanna with Acacia nigrescens, Sclerocarya birrea, Acacia tortilis, and Combretum apiculatum as some of the dominant woody species. Themeda triandra, Digitaria eriantha var. pentzii, Bothriochloa radicans, Eragrostis superba, Panicum maximum and Urochloa mosambicensis are the dominant grasses while forbs are few.

Coetzee (1983) distinguished another vegetational variation on gabbro between Skukuza and Tshokwane which he referred to as a Lannea stuhlmanni/Pterocarpus rotundifolius/Themeda triandra dominant shrubby tree veld. The same woody species that occur in the Sclerocarya birrea/Acacia nigrescens-savanna described by Gertenbach (1978) occur here but Lannea stuhlmanni, Pterocarpus rotundifolius and Combretum hereroense are prominent dominants in this variation.

Wildebeest usually occur over the majority of this landscape particularly after a fire, but the Chloris virgata/Acacia nigrescens shrubveld near Orpen is a highly preferred area for wildebeest which served in the past as the summer grazing grounds for the Western Boundary sub-population.

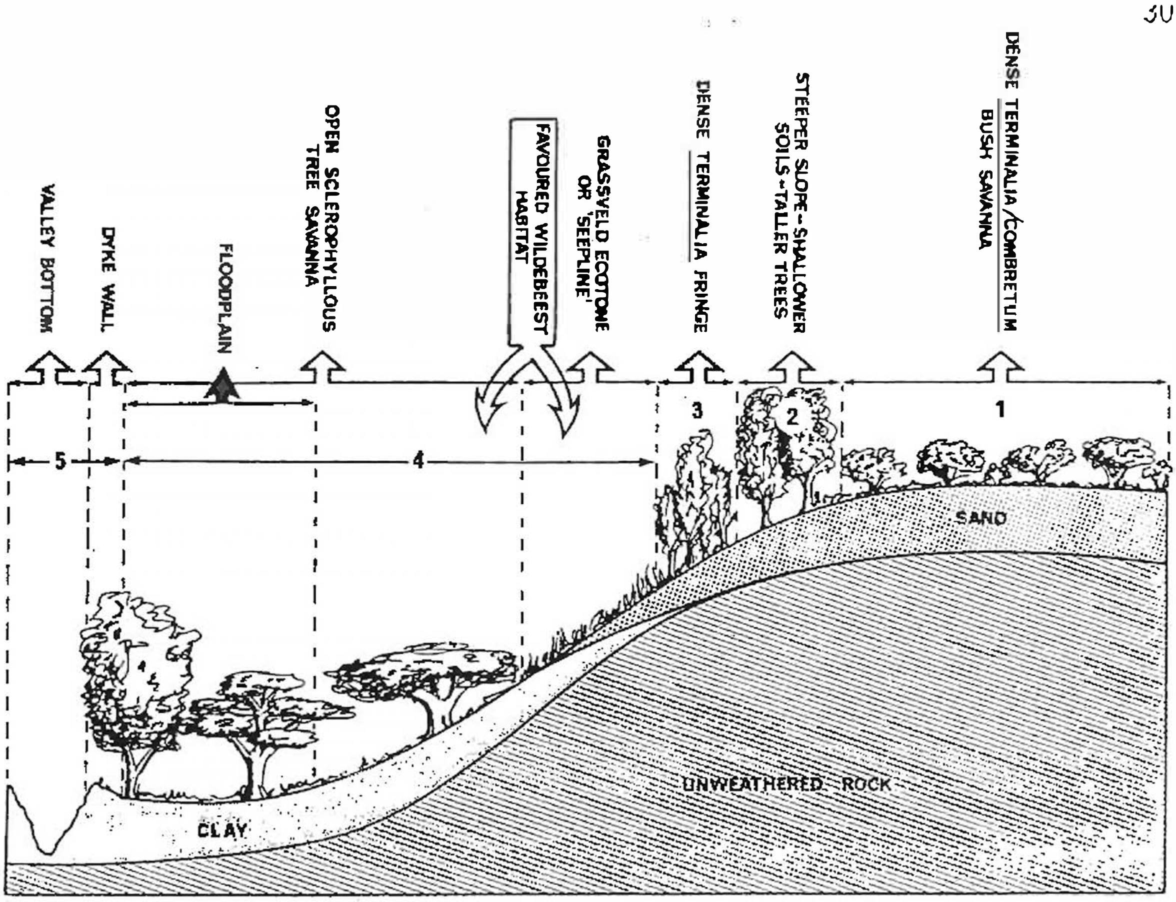
2.5.12 Mixed Combretum/Terminalia sericea Woodland

The geological substrata are granite and gneiss with numerous small dolerite intrusions (< 10m wide). The landscape is undulating with distinct uplands, ecotones and bottomlands.

This landscape has an interesting catenary sequence of soils that correspond strongly with position in the topography (Figure 2.5.2). Upland soils are deep, sandy and leached which support a dense bush savanna which consists of a Terminalia sericea/Combretum zeyheri/ Combretum apiculatum- community with a dense low and high shrub layer with few or no trees. Where the slopes become steeper and the soils more shallow, larger trees such as Sclerocarya birrea, Albizia harveyi and Acacia nigrescens are to be found.

On the ecotone or seepline where the convex topography changes to a concave topography, a dense fringe of Terminalia sericea trees occurs. This is followed down the catenary sequence by a zone of almost pure grassveld which can sometimes be as much as 100 m wide or more. These grasslands form "corridors" through this landscape which separate the dense broad-leafed bush savanna on the uplands and the sclerophyllous tree savanna of the valley bottoms. These corridors are important wildebeest habitats and in the past probably also served as migration routes for the sub-population which inhabited this landscape. This aspect receives more attention in the chapter on population trends.

The bottomlands of this landscape are open tree savanna with a dense grass cover if not overgrazed. Gertenbach (1983a) classifies it as an Acacia nigrescens/Combretum apiculatum association which is comparable to the vegetation of Landscape 2.5.4.



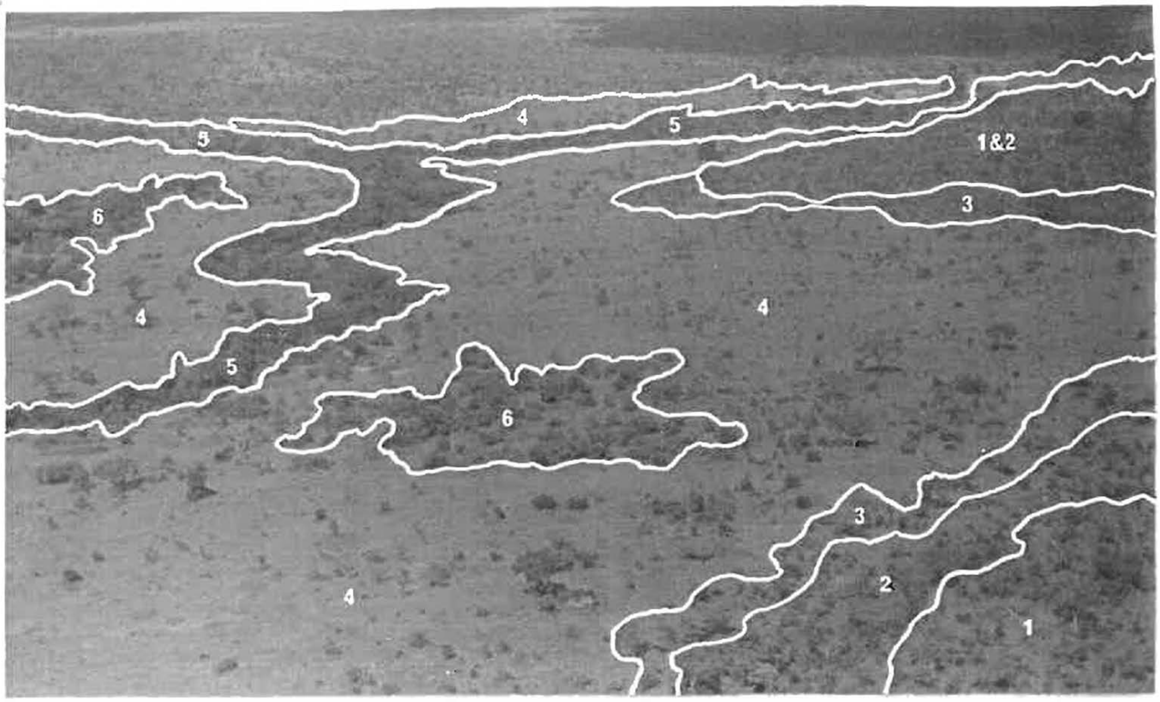


FIGURE 2.5.2: The typical catenary sequence of the Mixed Combretum/Terminalia sericea Woodland Landscape of the Kruger National Park showing the "seeplines" and open Savanna favoured by wildebeest. 1: Dense Terminalia/Combretum bush savanna on sandy crests; 2: Taller trees on the shallower soils on steeper slopes; 3: Dense Terminalia fringe above the seepline; 4: The seepline and open sclerophyllous tree savanna - habitats favoured by wildebeest; 5: Dense Acacia in valley bottoms; 6: Isolated Spirostachys africana/Euclea divinorum patches on brackish soils. The photograph shows one of the broad seeplines in the Ripape area.

2.5.13 Acacia welwitschii Thickets on Karoo Sediments

As was mentioned in the sub-section on geology, the CD consists basically of granite and gneiss in the west and basalt in the eastern half which are separated by a belt of Karoo sediments. These sediments form a distinct landscape of their own though it is seldom broader than four kilometres. The terrain is concave, low-lying and reasonably flat with slight slopes. In the KNP the landscape is unique in that the vegetation is dominated by Acacia welwitschii subsp. delagoensis which, apart from South Africa, only occurs in Swaziland and southern Zimbabwe.

The Acacia welwitschii-thickets can be divided into two variations on the basis of the grass species components of the field layer (Coetzee, 1983). This variation need not, however, be made here. A large variety of forbs is also present and this, as well as the grass composition indicate that this landscape is heavily grazed and the grass cover is therefore usually sparse.

The structure of the woody component is usually a moderate tree savanna with tall shrubs and sparse low shrubs but where the soils originating from Shales and Cave Sandstone mix, a complex of plant communities occur that consists of a combination of one of the varieties of the Acacia welwitschii community, and a Albizia petersiana var. evansii community. The latter community usually contains dense tall shrubs which over large stretches of this landscape form an almost impenetrable barrier to plains-loving wildebeest and this landscape thus separates the western sub-population from those on the east.

2.5.14 Kumana Sandveld

This small landscape lies just to the east of the Karoo sediments and in fact is also of Karoo sedimentary origin. The terrain is lightly undulating and the deep sandy soils carry a vegetation with a moderate to dense low shrub layer, a sparse tall shrub layer and a tree layer that is sparse to completely absent.

Sodium saturated soils occur where the shales appear on the surface, and on these soils *Acacia welwitschii* thickets, similar to those described for Landscape 2.5.13 are present.

In the north along the Sweni Spruit this landscape is fairly well used by wildebeest but in the southern parts they are rare due to the density of the shrub layer.

2.5.15 Sclerocarya birrea/Acacia nigrescens Savanna

This large landscape is characterised topographically by flat plains intersected by well-defined drainage channels. The soil pattern is therefore relatively homogeneous and no sudden changes occur in soil type over short distances.

The most important two components of this landscape are the *Sclerocarya birrea/Dichrostachys cinerea/Pterocarpus rotundifolius/Themeda triandra*-tree veld south of Tshokwane and the *Sclerocarya birrea/Acacia nigrescens/Themeda triandra/Bothriochloa radicans*-tree veld north of Tshokwane. This larger division is mainly attributed to the higher rainfall in the southern than in the northern sections of this landscape respectively, with the 550 mm isohyet as the reputed boundary.

Both of these components, however, are open tree savannas with moderate shrub layers and dense field layers.

The main difference between the two associations lies in the composition of the field layer. The sequence of dominance in the former component is Themeda triandra, Panicum coloratum, Digitaria eriantha var. pentzii, and Bothriochloa radicans, while the latter component has the sequence of dominance as Themeda triandra, Bothriochloa radicans, Digitaria eriantha var. pentzii, and Panicum coloratum. All the indications are that the latter is a drier variation of the Sclerocarya birrea/Acacia nigrescens Savanna.

Other associations described by Coetzee (1983) for this landscape are either very local or are secondary communities as a result of overgrazing (Gertenbach 1983a).

The Sclerocarya birrea/Acacia nigrescens savanna forms the heart of the wildebeest and zebra habitat in the CD. These animals migrate annually between the northern and southern parts of the landscape (Smuts, 1972 & 1974b; Braack, 1973; Whyte 1980). Summers are spent in the north in the Sweni/Lindanda area and the winters to the south in the Mlondozi/Sabie River area. The annual migration thus takes place between the two most important variations of this landscape.

2.5.16 Lebombo South

This is an undulating landscape with ridges and bottomlands running north/south. The Lebombo Mountains are almost 100 metres higher than the adjacent basalt plains and sometimes form escarpments on the western slopes.

Wildebeest do not favour this landscape probably as a result of the rocky nature and steep gradients of the terrain, but in the south and to the east of the mountain Muntshe, the Lebombo Mountains flatten to more gentle gradients and wildebeest can occur in some numbers, particularly after fires and when the migrants are in the south of their range in winter.

2.5.17 Thickets of the Sabie River

As the name indicates this landscape is low lying and is characterised by a dense woody vegetation which could be referred to as an Acacia nigrescens/Combretum apiculatum association Pienaar (1963) refers to it as "dense thornbrush thickets" and as such they are almost totally avoided by wildebeest.

2.6 FIRE

The frequency of natural fires caused by lightning in the KNP is ample evidence that even before the advent of man, veld fires were an integral part of the ecology of the erea. The KNP, however, has probably been subjected to unnatural fires caused by man for many hundreds of years as even the Bushmen reputedly used fire to facilitate their hunting (Gertenbach, 1983b). Subsequently various Bantu tribes and later still the first white men also used fire to assist hunting and to clear tall grass and bush to improve grazing for domestic stock.

Since the proclamation of the KNP in 1926, various veld burning policies have been adopted which have varied from the practice of burning annually to a policy of complete protection from fire. Nowadays, however, a system has been adopted which attempts to simulate the natural fire regime (i.e. the same frequency of occurrence as that of naturally ignited lightning fires) (Gertenbach, 1983b). During wet cycles there is a faster build up of grass fuel and thus lightning fires would occur more frequently than in drier cycles where there is a much slower accumulation of inflammable material. Thus a more flexible burning programme has been developed with longer or shorter intervals between burns which are dependant on the amount of inflammable material.

The KNP is divided by a system of firebreaks into 400 burning blocks of which there are 126 in the CD.

As the landscapes of the KNP are now considered the basic management units, all burning blocks from each landscape are thus grouped together. Depending on the management objectives for each landscape (Joubert, in prep. a) and the amount of inflammable material in the standing crop, the percentage of the landscape to be burned is then decided upon and the blocks to be burned are allocated. This is done chronologically - the blocks which have stood unburnt for the longest period being burned first.

For management purposes lightning fires or "accidental" fires caused by tourists, poachers etc. are considered as normal controlled burns and as such a block burned in this way falls into the chronological sequence for its next burning treatment.

2.7 FAUNA

The numerical status of the larger herbivorous species is determined annually by means of two aerial censuses. The first, which is locally called the "aerial census", is conducted by helicopter and is restricted to the counting of only the elephant and buffalo populations. This census is conducted in August. Hippo are also counted annually using a helicopter. The second, known as "aerial ecological surveys" makes use of a six-seater fixed wing aircraft and the numbers and distribution of all other larger mammals are recorded (Joubert, 1983b; in prep. b). This survey, which covers the whole of the KNP by flying strips of 800 m wide (with the exception of the mountainous regions around Punda Maria and Malelane) takes about four and a half months and lasts from May to September. The most recent population estimates from the censuses of 1984 are given in Table 2.7.1 (Joubert, 1984).

Table 2.7.1: Population estimates for the larger herbivores in the Kruger National Park (KNP) and the Central District (CD) in 1984.

SPECIES	TOTALS		% IN CD
	KNP	CD	
Impala (*Aepyceros melampus*)	138 951	47 757	34,4
Buffalo (*Syncerus caffer*)	24 585	6 467	26,3
Elephant (*Loxodonta africana*)	8 273	2 093	25,3
Zebra (*Equus burchelli*)	30 457	12 830	42,1
Wildebeest (*Connochaetes taurinus*)	11 933	8 026	67,3
Kudu (*Tragelaphus strepsiceros*)	9 161	3 201	34,9
Giraffe (*Giraffa camelopardalis*)	5 368	3 250	60,5
Waterbuck (*Kobus ellipsiprymnus*)	3 285	1 222	37,2
Warthog (*Phacochoerus aethiopicus*)	2 834	1 228	43,3
Sable antelope (*Hippotragus niger*)	1 959	316	16,1
Tsessebe (*Damaliscus lunatus*)	930	46	4,9
Roan antelope (*Hippotragus equinus*)	344	1	0,3
White rhino (*Ceratotherium simum*)	887	104	11,7
Black rhino (*Diceros bicornis*)	104 *	26 *	25,0
Hippopotamus (*Hippopotamus amphibius*)	2 353 ***	- **	-
Eland (*Taurotragus oryx*)	797	6	0,8

* Hall-Martin (1984).
** Not included, as major populations occur only in rivers which constitute CD boundaries.
*** Whyte (1984).

Most of the above species have been the subject of study to a lesser or greater degree. These studies include: buffalo (Pienaar, 1969a); elephant (Smuts, 1975a); impala (Fairall, 1971; Whyte, 1976); zebra (Smuts, 1972, 1974a); wildebeest (Braack, 1973); giraffe (Fourie, 1977); roan antelope (Joubert 1970, 1976); tsessebe (Joubert, 1972) and hippopotamus (Pienaar, van Wyk & Fairall, 1966a; Smuts and Whyte, 1981). All of the large mammals of the KNP have also received some attention in Joubert & Hall-Martin (in prep.).

Pienaar (1969b) and Smuts (1975b) conducted general predator/ prey studies while more specific studies include those on lion (Panthera leo): Bryden (1976); Smuts (1976a, 1976b, 1978a); Smuts, Hanks and Whyte (1978); Smuts, Anderson and Austin (1978); Smuts, Whyte and Dearlove (1977, 1978); Smuts, Robinson and Whyte (1980); Whyte (in prep. a); wild dog (Lycaon pictus): Reich (1981); leopard (Panthera pardus): Bailley (in prep); and spotted hyaena (Crocuta crocuta): Henschell (in prep.).

Inventory surveys have done much to clarify the status and distribution of some other faunal groups and literature arising from these include: small mammals (Pienaar, Rautenbach & de Graaff, 1980); reptiles (Pienaar, Haacke & Jacobsen, 1978); amphibia (Pienaar, Passmore & Carruthers, 1976); fish (Pienaar, 1978); butterflies (Kloppers & van Son, 1978); birds (Kemp, 1974; Newman, 1980); and insects (Braack & Bannister, in press).

CHAPTER 3

RECENT HISTORY OF THE WILDEBEEST POPULATION

This sub-section covers the period from the inclusion of the CD under the administration of the Sabie Game Reserve in 1903 to the start of the fieldwork for this project in January 1978.

Almost the only sources of information from the early part of this period are the annual reports of the Warden Col. James Stevenson-Hamilton and in 1903 he had this to say: "Blue wildebeest once existed in large numbers throughout the Reserve, parts of which are eminently suited to their habits; these animals have been so shot down that only some three troops of ten to twelve members each, and a few old solitary bulls, who generally run with the herds of impala, are left. However, a few years will set them on a good footing once more" (Stevenson-Hamilton, 1903).

Due to the initial scarcity of game Stevenson-Hamilton and the early Rangers instituted a policy of predator control with the intention of allowing the game populations of the KNP the maximum possible growth potential. Nearly all the predatory species were implicated including species like wild dog, crocodile (*Crocodilus niloticus*), cheetah (*Acinonyx jubatus*) and even raptorial birds like the martial eagle (*Polemaetus bellicosus*). This culling policy remained in force until 1958 and eventually accounted for 2 846 lions over the whole KNP during the 55 year period giving an average of 52 lions per year (Smuts, 1975b). Data on the number of lions shot in the CD alone are not available. In addition many other lions were shot just outside the boundaries, some of which must have been KNP lions. The effect of this culling is unknown but must have had some influence on the prey populations (Smuts, 1975b).

By 1912 the situation for the game species had improved greatly and Stevenson-Hamilton could report: "It is rather a difficult matter to hazard any statement as to the numbers of each species (in the Sabi Reserve *) ..... I think however that the following, allowing for unavoidable inaccuracies, gives a fair estimate of the numbers as they stand at present ..... Wildebeest 3 000... " (Stevenson-Hamilton, 1912).

The period between 1916 and 1923 however seemed to have brought an increase in mortality as Stevenson-Hamilton (1939a), in a report to the South African Veterinary Medical Associations stated " In 1916 many wildebeest (and other game), all species which had been increasing progressively since 1902, died, after a long drought, in considerable numbers in the vicinity of waterholes. In 1922-3 wildebeest .... died during heavy rains ....".

In 1923 a large portion on the western side of the CD was excised from the Park which was to have a serious effect on migratory game in later years when the western boundary was fenced. This fence when it was erected, cut the area utilized during the seasonal migratory movements of the wildebeest and zebra roughly in half and totally disrupted the migratory pattern with disastrous results in the long term. This fence, and the opinions and convictions of those in agreement with or opposed to the fence's erection, of necessity must receive some attention, but will be reviewed later in this sub-section.

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* Note: This spelling of the name "Sabi" was used by Stevenson-Hamilton and other early writers but has now been generally accepted as "Sabie".

By 1925 however the situation for the wildebeest population had apparently once again improved as Stevenson-Hamilton (1925) could report. "In my annual report of 1912 I attempted a very rough estimate of the number of game animals present in the Reserve. I have reason to believe that my calculations were then considerably under the mark and since that time, the total has increased at least four fold, .. . Blue wildebeest is now the most numerous species at present found in the Reserve"

This state of well-being persisted for a few more years followed by a period of decline. Stevenson-Hamilton (1939a) gave his reasons: "There was a rapid and uninterrupted general increase among blue wildebeest up to about 1932, when so high a peak was reached that much of their favourite grazing country became overstocked, and the pasture was so much destroyed by overgrazing combined with drought, that it has not yet recovered. Since that time there has been a visible decline in the numbers of wildebeest in the eastern areas of the Park though in the western ones they are as numerous as ever, and I am inclined to attribute this decline to migration due to overgrazing rather than to any pathological cause".

In 1933 reference was made to game migrations west- and eastwards to find water and pasture. It was pointed out that animals were noticeably absent in the Central District (Satara and Tshokwane sections) and that the area around Tshokwane, where there were permanent waterholes, was severely overgrazed. "On the other hand the country outside the Park between Acornhoek and Rabelais was full of game. This winter trekking is no new thing, though seven years of drought in the Park have caused it lately to happen on a larger scale than formerly.

There was always a tendency for the herds to move westwards from July onwards until the first rains, but up to 1923 the western areas were part of the Sabi Game Reserve so that the animals did not by trekking have to leave their own country. Now, owing to the width of the Park not being sufficient for winter trekking requirements we lose a large number of our animals for several months of each year" (Stevenson-Hamilton 1933).

The annual report of 1934 again made reference to a westward movement of wildebeest from the CD. "From Satara to Rabelais Gate game was almost absent ..... Large numbers continued to trek out westwards into adjoining farms in search for water and grass" (Stevenson-Hamilton, 1934).

In 1936, Stevenson-Hamilton had recognised the future problem of zebra and wildebeest moving westward out of the CD and possibly even eastward into Mocambique and said: "It is unfortunate that the portion of the Park lying between the Sabie and Olifants River does not allow sufficient space for the animal migrations of animals in search of fresh pasture. Like all other ruminants game animals must have seasonal changes of feeding grounds. As the area which they have been frequenting becomes worn and soiled, they move to another one. In winter when the dry eastern areas of the Park no longer provide sufficient nourishment there is a general move to the better country westwards. This has always been a marked feature during the past 34 years, but became accentuated in the seasons of exceptional drought such as 1911-1913, and 1933-1935. Before 1925 these western areas were all included within the Sabi Game Reserve, which thus provided ample space for migration; but after their excision, there remained only a long strip between the Sabi and Olifants Rivers, of some 25 to 50 miles in width, which of course is not nearly adequate for the requirements of large numbers of animals which are no longer able to supply themselves in their summer feeding grounds. The Park area is probably the main breeding ground, since ample food is available in all but exceptionally bad summers, but when winter comes the veld is no longer able to support the same number of animals as formerly, and in consequence the large herds of e.g. wildebeest first break up into smaller parties in search of food, and finally wander away west and east partly into Portuguese Territory where conditions are better, but mainly towards the west in the direction of the better watered and more fertile country nearer the foothills of the Berg" (Stevenson-Hamilton, 1936).

Between 1932 and 1943 there seemed to have been a fairly steady decline in wildebeest numbers and this was ascribed to drought, migration, hunting pressure outside the KNP and bush encroachment. The following extracts from annual reports are of relevance.

"The rains at the time of the 1937-38 breeding season having completely failed, the latter was a serious catastrophe for all (grazers). There was no grass either when the females where parturient or after the birth of the young, and therefore these in the vast majority of cases died where the mothers had not previously aborted. This was the case nearly all over the Park including even the usually prosperous western area. I have not seen so few .... wildebeest calves for years, not even in the terribly serious drought at the end of 1935" (Stevenson-Hamilton, 1938).

"Within a radius of 10 miles of this place (Tshokwane), there existed in former days, probably a larger stock of game animals than within any other area of the same size in the Sabi Game Reserve; lions were also exceedingly numerous. Between 1920 and 1926, the Warden alone killed over 100 lions within the above radius, with the ultimate result that there occurred an enormous increase in the wildebeest which, up to about 1930 swarmed there and completely devastated the veld; the outcome in combination with the long drought, being that the roots of the grass were destroyed, and the ground lay as bare as a roadway .... After 1930 the wildebeeste and other game gradually left the area, which is now nearly denuded of the larger animals " (Stevenson-Hamilton, 1939b).

"Wildebeest suffer from being accorded no special protection outside the Park, where any number may be killed by farm owners or lessees for lion bait etc. In consequence the herds suffer severely when outside the Park during migratory periods" (Stevenson-Hamilton, 1942).

In his 1943 annual report Stevenson-Hamilton stated that "wildebeest are definitely less numerous than they used to be in the eastern and central portions south of the Olifants River", and attributed this to "the spread of the thick bush and the consequent decrease in the amount of open grazing which is becoming increasingly manifest all over the Park". Joubert (in prep. a) however points out that these statements were made at the end of a wet cycle which could have given rise to the spread of thick bush. In his subsequent report, Stevenson-Hamilton (1944) admits that his previous statement on bush encroachment was not as universal as he had presented it and had in fact in some places even receded (Joubert, in prep. a).

And in 1945: "..... I do not think there has been any noticeable increase (in the wildebeest) between the Sabi and Olifants for some years ..... I attribute the static condition and even decrease of these animals to the persecution they are subjected to outside the Park, where they are regarded as vermin, and destroyed wholesale by whites and natives alike. They are also, more than other species, the victims of lions both inside and outside the Park; but without doubt it is human action which is mainly responsible and being migratory, they are exposed to this through being so frequently outside the sanctuary" (Stevenson-Hamilton, 1945).

In 1945 Stevenson-Hamilton attended a meeting with farmers affected by the depredations of game in some form or other and, although he found them generally sympathetic, he said of the meeting: "The general impression left on my mind was that, with civilization closing in on all sides, ultimately something must be done to segregate the game areas from those used for farming; otherwise sooner or later some excuse for liquidation of the wild animals will be found. Of course it would not suffice to segregate the K.N. Park without including the game area lying to the west between the Sabi and Olifants Rivers. This extends some 20 miles west of the Park Boundary, and forms the migration space for a great deal of the Park game during the dry season .... Any game fence or other obstacle designed to segregate the game from the farming areas should include this stretch of country which comprises more or less the part of the Sabi Game Reserve deproclaimed in 1923, and since not found suitable for permanent white settlement. It is in fact largely made up of farms the property of absentee owners who use them as hunting grounds for a few months each year" (Stevenson-Hamilton, 1945).

It is clear that Stevenson-Hamilton appreciated the potential effects of fencing-out the game area to the west of the CD and, although this was his last year before retirement as Warden of the KNP, his successor, Col. J.A.B. Sandenbergh, supported Stevenson-Hamilton's ideas on this issue and states in his first annual report: "I am certain that sooner or later some means must be found to confine the game to the Park if we are to ensure the existence of all species. I suggest that there is urgency and that the whole question of segregation of game from farming areas should be gone into at the earliest possible date" (Sandenbergh, 1946).

In the annual report of 1947, Sandenbergh once again mentions the westward movement of game at the height of the drought and also of the magnitude of hunting outside the KNP's boundaries: "The Satara and Tshokwane sections lost a lot of game to the west, and, at the height of the drought I personally saw thousands of head of game moving out of the Park towards the Sand River to drink ..... From Buffelshoek northwards, thousands of head of game moved out in the direction of Klaserie and hundreds of shottists descended on the game and, had it not been for the police patrols, these herds of game moving in search of water and grazing would have been decimated. During the year, senior representatives of Native Affairs agreed that it would serve both Agricultural and Pastoral interests on the one hand and Game Preservation on the other hand if the western boundary of the Park could be fenced adequately. From conversations I have had with senior officials of all Departments affected by the clash between Game Preservation and Farming interests, I consider that the ultimate answer to the question of protecting farming interests and ensuring protection of the game is, without doubt, fencing of the type recommended by my predecessor in his report for 1945" (Sandenbergh, 1947).

By 1947 then, the idea of fencing the western boundary had become firmly entrenched and was seen by all Departments involved as the answer not only to the protection of the migratory herds, but also to the protection of agricultural interests outside the KNP.

Inside the CD however, the declining trend in the grazer populations, initially reported by Stevenson-Hamilton (1943), continued, and by 1953 Steyn, by then Warden of the KNP, reported: "*... the most pertinent and alarming phenomenon which has been in progress for about 10 years, still continues. This phenomenon is the decrease amongst the pure grazers, e.g. sable antelope, roan antelope, tsessebe, waterbuck, wildebeest, zebra and reedbuck, in contrast with the increases amongst browsers, e.g. impala, giraffe and elephant. The gain amongst these species does not weigh up against the loss amongst the former.... This phenomenon is more apparent in the southern areas (south of the Olifants River) than in the northern areas according to the rangers' reports, and ties up with the fact that predator control was applied for a longer period (except Letaba Section) in the north than in the south" (Steyn 1953).

The decline in the grazers continued according to Steyn (1954) and he also mentions that zebra were now in the majority whereas wildebeest had previously been more numerous than zebra.

In this year, also, a report was submitted by members of the Biologist's Section of the KNP and the Dept. of Veterinary Services which reviewed possible game-proof barriers which could be used on the western boundary (Nel, Meeser & van der Schyff, 1954). The recommendations of this report were that the fence should be of the basic "red-line" type (multi-strand barbed wire).

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* Translated from Afrikaans

In the following year, the first, and apparently only, voice of dissent expressing opposition to the fencing of the western boundary was raised by a group of game farmer/landowners to the west of the CD's boundary. At a meeting held in July 1955, a Committee was appointed to "negotiate to obviate the fencing of the western boundary of the Kruger National Park and to get the "red-line" adopted, if possible, or some similar line (further west) conveniently suitable to the interested parties", and this Committee drew up a memorandum outlining their objections and proposals. In this memorandum it is stated that: "It is the considered opinion of many of the most senior and experienced game preservationists in South Africa that the permanent narrowing of the Kruger National Park game area (in this narrow section of the Park) by erecting a barrier on the western boundary between the Sabi and Olifants Rivers, will very materially reduce the game in the Kruger National Park by the restriction of its annual east/west migration in search of water and grazing", and that, "Upon such a decision being made (to fence the western boundary) this Committee would wish to make the strongest possible plea that as large an area as possible of the private reserves be included with the Park" (Mackenzie, 1955).

However, after a preliminary study of the game movements in this area, two of the KNP's Biologists concluded: ".... it is clear that the Sand River is the primary factor in the movement of game across the border during the dry season when the temporary streams such as the Lipape (Ripape) and Mutlamubi (Mutlumuvi) have lost their water. If water supplies in these streams can be made adequate, fencing will be entirely practicable" (Nel & le Roux, 1956b).

In a further memorandum Nel and Meeser (1956) pointed out that:

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In a further memorandum that year Nel and Meeser (1956) pointed out that:

"* (b) The Transvaal Provincial Council had once again recommended the fence on 9th December 1949.

(c) On 18th March 1949 the Lowveld Farmers' Union repeated their appeal and elected a Committee to make recommendations regarding the fence.

(d) On 7th May, the (KNP's) Biologist had recommended the fence.

(e) Nel, Meeser and van der Schyff (1954) had recommended a barbed wire fence as the basic game-proof barrier".

As a result of these appeals and recommendations, Nel & Meeser (1956) once again recommended: "* Both hunting and agitation (to fence the boundary) have been intensified as a result of, among other things, the repeated occurrence of foot-and-mouth disease among domestic stock, the trampling of domestic stocks' grazing by game and the competition by game at the waterholes .... for the sake of good neighbourliness with the farmers, as well as for the protection of the game itself, the Game Reserve will have to be fenced".

Thus although there was a plea to the contrary by interested game farmers it was felt that it would best suit the majority of interested parties to fence the western boundary and, provided the necessary conservation measures were taken, there would be no harm done to the game populations.

By this time it was generally accepted that the fence would become a reality and a start was made with the provision of artificial

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* Translated from Afrikaans

water points which were to replace the Sand River which would be excised by the fence. During the years 1955 to 1959 the following dams were built (Pienaar 1973b): Vutomi (1955); Ngwenyene (1956b); Lugmag and three smaller dams at Ripape (1957); Shisakarangondzo (1958); and Tswiriri and Nwanitsana (1959).

As regards population trends, the reported decline seems to have ended during the winter of 1956 as the 1957 Annual Report stated: "In the Central District however, conditions were more encouraging. During the winter, large numbers of wildebeest moved in from the west and the remaining herds increased noticeably" (Anonymous, 1957).

In 1958 the improvement continued: "* In the Central District good progress has been observed and the new dams in the Lipape-Manzentonto area held the large herds of wildebeest in that area back longer than normal in the latter part of the year. Elsewhere they were well distributed throughout the District and a very large concentration behind Nwamariwa koppie (a few kms east of Tshokwane) made the area look as it did during 'the old days'" (Steyn, 1958). This is the first reference to a concentration among the wildebeest of one of the other sub-populations and is important because of the implication that such concentrations also occurred in earlier times in that sub-population.

It is important at this stage to examine what was known about the movements of the Western Boundary sub-population before the fence was erected. Initially it was supposed by the earlier Wardens of the KNP that the movement was westward during the winter followed by a return to the east in summer (e.g. Stevenson-Hamilton, 1924; Sandenbergh 1947).

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* Translated from Afrikaans

It is of course extremely difficult to understand and interpret animal movements without the benefit of a number marked animals and regular subsequent attempts to resight these animals. Descriptions of the movements of wildebeest given by Stevenson-Hamilton and Sandenbergh, as a result of them not having had the benefit of such marked animals, were probably incorrect as their description of the general westward movement from the CD in winter is in contrast to the "northwest in summer/southeast in winter" movements described by subsequent workers (Braack, 1973; Pienaar, 1960; Smuts, 1972). South of the Sabie River (outside this study's area) the migratory pattern may well have been west-east from the Pretoriuskop area in summer to the foothills of the Drakensberg with the worsening of conditions due to the winter. The area to the west of Pretoriuskop was excised from the KNP in 1923 and although bush encroachment has been given the blame for the decline in wildebeest numbers in the Pretoriuskop area (Sandenbergh, 1950), human development, increased hunting and poaching and the ever decreasing access to the winter grazing in the excised area must have played an equally if not more important role. Stevenson-Hamilton's references to the westward movement of wildebeest in winter were probably mainly pertinent to this more southern population but this is not always entirely clear from his annual reports.

However, Stevenson-Hamilton's earlier reference (1934) specifically stated that game had trekked <u>westward</u> in search of water and grass while in the Satara/Rabelais area game was almost absent. This implies that at that time in the CD the winter movement <u>was</u> in fact westward.

It is possible therefore that movement patterns may have changed since 1934. Perhaps gradual developments and increased hunting pressure outside the sanctuary had enforced a change which was never documented. Nel & Le Roux (1956a) also detected this anomaly and, after a study of game movements in the area, concluded:

a)" *.... it appears that the 'traditional winter migrations to the west' did not in fact take place or do not at present take place".

b) Other movements to the west as a result of drought e.g. 1911 to 1913 and 1933 to 1935, were not migrations but temporary evacuations of activity zones (woonbuurtes) followed by a return to the well known territories in the Reserve once conditions became more favourable.

g) We are also of the opinion that because no large scale movements occur to the west, the fencing of this part of the boundary is practicable provided the necessary conservation measures are met (e.g. provision of water), even though the boundary at present cuts through typical wildebeest and zebra territoria at A (Jeukpeulhoek) and B (Sarabank)". (Refer to Figure 3.1.1. on page 54).

The movements of the wildebeest in this area were discussed more fully in a separate memorandum (Nel & Le Roux, 1956b) in which they identified the Jeukpeulhoek/Sarabank area as the summer grazing area with the winter grazing area around Ripape (Lipape). As the waterholes around Ripape dried up the wildebeest would trek all the way to the Sand River at Mala-Mala to drink and back again - a round trip of approximately 20 km. This they established by actually following herds that had come down to drink in the Sand River back to the grazing grounds.

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* Translated from Afrikaans.

Pienaar (1958) reaffirmed this, though probably basing his statements on the writings of Nel & le Roux and states: "* ... Spatio-temporal movements of wildebeest in this area can be correlated with great regularity to the drying up of the natural waters in the late winter and the subsequent large scale movement to traditional communal drinking sites in the Sand River outside the boundary of the Park. The cows are then usually pregnant and after the first spring rains there follows a movement to the north-east where the animals calve in the Jeukpeulhoek/Sarabank/Mahlobyanine area and then later in the summer disperse once again to the south and further eastwards."

Of the Sweni/Mnondozi sub-population in the same year he reported: "*The zebra and wildebeest concentration between Nwamuriwa and Lindanda repeated itself in January and February but was less intense than that of last year. The movements here will be watched with interest as the Mnondozi area is very dry and the dam is virtually empty". This second reference to this sub-population is also of interest as it is the first mention of their north-in-the-summer/south-in-the-winter migration.

The Satara sub-population also receives its first mention in the annual report of 1958: "* Large numbers of wildebeest and zebra once again visited the Shinkelengane area of the Satara Section as in the past".

By the early 1960's however, the KNP's Biologist had come to recognise that the migration on the western boundary extended far further north in the summer than had previously been reported, and Pienaar (1960) drew an unpublished but comprehensive map of the movement patterns in the

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* Translated from Afrikaans.

area between 1957 and 1960. This map has been reproduced here (Figure 3.1.1), and clearly shows the summer and winter grazing areas and migration routes. These routes and patterns are also described in the Annual Report of 1962 (Anonymous, 1962). Further information on the map which could not be included for lack of space was the time of year when wildebeest were encountered at various localities. Briefly these are as follows: In January, February and March the concentrations were found in the CD north of the Timbavati River in the area to the west of Hartebeesfontein Dam as well as on the game farms Adger, Rothesay, Vlakgesight, Johniesdale, Lillydale and Kempiana. This area forms part of the "Acacia on gabbro" Landscape (see Chapter 2) and is the heart of the Chloris virgata/Acacia nigrescens shrubveld community which Gertenbach (1978) describes as "a highly preferred area for wildebeest".

With the onset of the winter in March/April and the accompanying drying up of the area the move to the south and east began and March-April found them in the Jeukpeulhoek/Mahlobyanine/Sarabank area. In May, June and July they could be found in the Ripape/Airforce Dam area on the wide seeplines which occur in that area, but from August to October they had moved further south to the Tswiriri Dam area in the CD but moving to and from the Sand River on the outside of the CD through the farms Eyrefield, Malamala and Flockfield.

After the first spring rains the concentrations began their northward move and Pienaar's map shows them to be in the Gowrie/Tswayini area in November, the Mahlobyanine area in December and back again to the north of the Timbavati River from January to March.

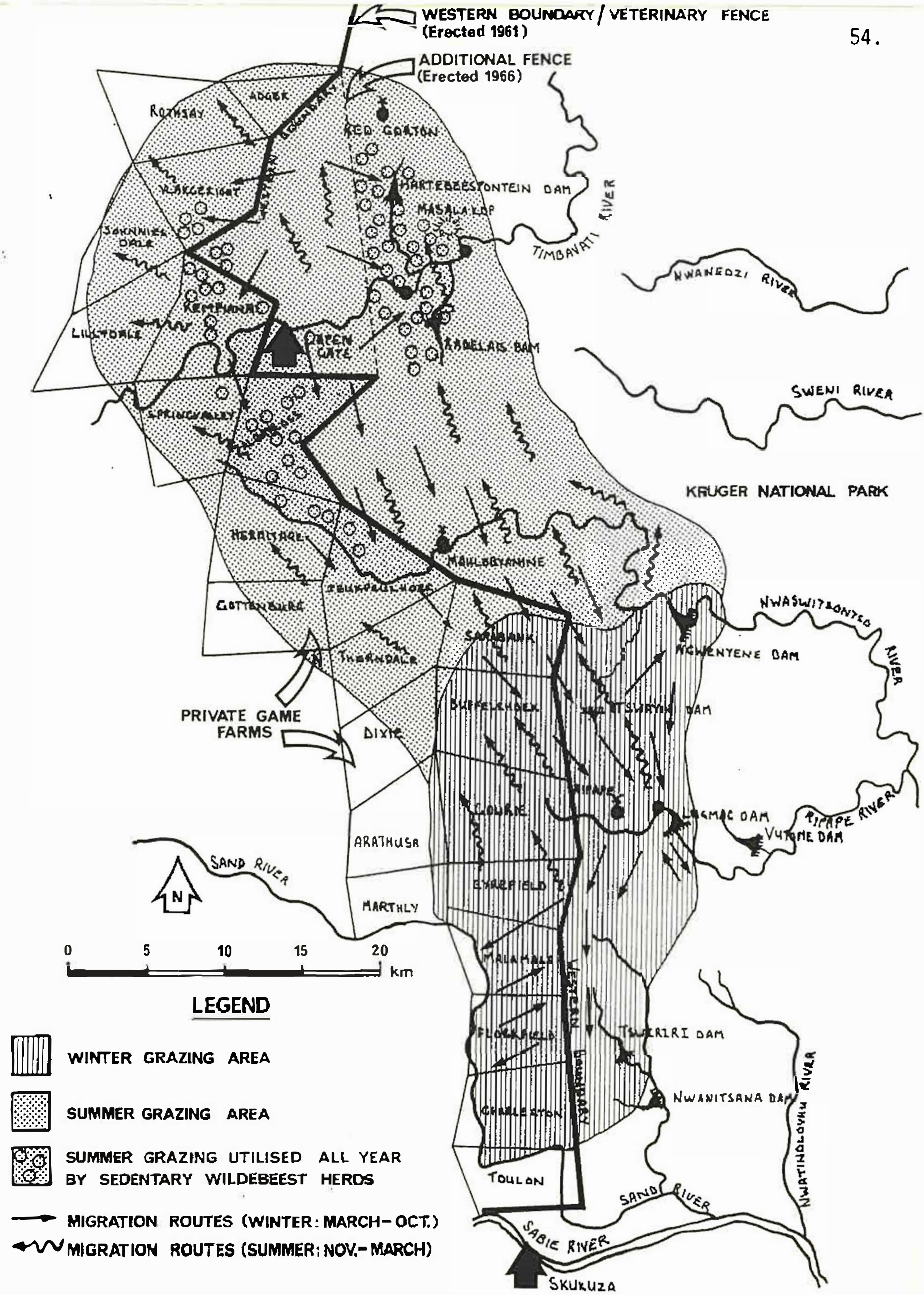

FIGURE 3.1.1 The migratory patterns of wildebeest in the Western Boundary sub-population as understood in 1960 (from Pienaar, 1960) showing the position of the boundary and proposed fence relative to the area utilized by this sub-population.

This would seem to have been the age-old normal pattern before the advent of man's interference and in normal years the functioning of this ecosystem could be summarised as follows:

The large gabbro areas in the Orpen/Timbavati area, with their short grassveld open plains and palatable grasses formed the choice part of the wildebeest range to which they would move as soon as the spring rains brought water to the area. The extent of these gabbros is well illustrated in Joubert (1983a). The drying up of this area forced the herds to move southeastwards to the broad seeplines in the Ripape area which supported highly palatable grasses on the wide grassveld seams growing on the sodium rich soils below the seepline itself. From a vegetation point of view, these broad seeplines are structurally also a highly preferred habitat for wildebeest and though it required a trek (possibly daily) of approximately 10 km to water and back (Nel & le Roux, 1956b), it was the closest "optimum" area from which the permanent water supply of the Sand River could be reached. Seeplines do occur further to the south but are narrower and thus are less suitable as wildebeest habitats. However, they probably served as useful open "corridors" through which the herds could trek to and from water in the Sand River.

As soon as the rains came, the wildebeest would immediately move back to the north west. Kloppers (pers. comm.*) informed me that one year he had stationed Rangers in the wildebeest concentration at Ripape just before the rains with the objective of following the herds once the rains arrived. The first rains were heavy and almost overnight the herds trekked all the way back to the gabbros to the north of Orpen.

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* Kloppers, J.J. Head: Wildlife Management, Private Bag X402, Skukuza, 1350.

This was also briefly described in Anonymous (1962).

This pattern would probably have persisted during normal years and only in times of excessive drought would the migration have deviated and moved west in the winter instead of southeast (Nel & le Roux, 1956b).

Severe outbreaks of foot-and-mouth disease in the KNP during 1958 proved decisive in the fence controversy, and as a result the Department of Veterinary Services obtained a grant from the Government for the purposes of erecting the game deterrent fence along the boundaries (Pienaar, 1973b).

Two new dams were built in 1959 namely Tswiriri and Nwanitsana and the provision of artificial waterpoints and the prevailing veld burning policy began to effect the migratory pattern. In that year's annual report (Anonymous, 1959) the following statements illustrate this. "* The general impression was that these artificial control measures had had a definite effect on the trek rhythms of these animals which were especially characterised by desultory and restless movements to and fro through the habitat where beforehand their regularity could be predicted with great accuracy."

Work on the boundary fences commenced during 1959 and the western boundary was "closed up to Ripape" (Anonymous, 1961) by the time of writing that report. Ranger's reports quoted here from this report indicate that initially a chaotic situation arose when the migratory herds arrived at the fence:

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* Translated from Afrikaans.

"* Go up the boundary from Ripape to Sarabank and find the fence in tatters...... In two places the wildebeest had flattened the fence with poles and all ... one of which was 200 yards wide (3.10.1960)."

"* The fence itself is lying in tatters and the blacks who are supposed to maintain the fence do not know where to start (15.11.1960)".

"* There are huge herds of wildebeest and zebra along the boundary between Sikkeltowkloof, Blackberry Glen and Orpen. They break the fence going backwards and forwards between water and the summer grazing on the farms (28.11.1960)."

A more dramatic account of the effect of the fence is given by Adendorff (1984) "... the game routes of bygone days were cut off (the movement of game going from east to west and vice versa) by this sudden barrier. I saw wildebeest and zebra massed against the fence, some wanting to come and others wanting to leave. Carnivora were in the pink of conditions as they did not have to hunt, simply chasing their prey into the fence. The animals could not comprehend and they congregated at the fence, dying of thirst and hunger and remaining there to rot. The carnivora could not cope with the situation and the stench from the carcasses was terrible. It took the herds a long time to accustom themselves to the fence and I found many giraffe which had died after being trapped between the strands of wire". It is possible that this is somewhat dramatised but it does illustrate the severe initial impact that the fence had on the population.

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* Translated from Afrikaans.

These quotes again stress the importance of the farms to the west as the summer grazing area, and the herds fenced inside the CD in the Orpen area began to have a serious effect on the grazing when access to these farms was denied them. Anonymous (1961) reports: "* During a visit at the end of February after the rains, I was shocked to see the condition of the grazing on the dolerite (gabbro) soils around Kingfisherspruit. Unmistakable signs of overgrazing are already evident and the veld is criss-crossed by hundreds of wildebeest paths".

These conditions as well as the severe drought of that time also highlighted the water shortage - thousands of animals had been fenced in to the area with insufficient water supplies. The water shortage became more acute by the day and a crash programme was launched whereby 36 boreholes were drilled in the crisis area of which, fortunately, a good percentage were successful and a catastrophe was averted (Pienaar, 1973b). Water was even carted to waterholes in tankers to help alleviate the problem and although there were some mortalities among wildebeest and zebra, no large-scale die-offs occurred similar to those experienced on the farms outside the KNP (Anonymous, 1963).

It would seem that much of the disturbance caused by the fence arose in the Jeukpeulhoek/Mahlobyanine/Sarabank area where the fence's direction is basically north-west/south east (see Figure 3.1.1) and much of the damming up of the migratory herds occurred here during the southward migration (Anonymous, 1962). Another manifestation of the disturbance was that during 1962 large concentrations of wildebeest moved south right down to the Sabie River and eastwards to Nwatindlopfu mouth for water - a previously unheard of occurrence (Anonymous, 1964).

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* Translated from Afrikaans.

The Annual Reports of 1962 and 1963 give accounts of minor, weather related movements of the Western Boundary herds and also describe deteriorating grazing conditions due to drought and overgrazing. Conditions on the farms to the west of the fence were even worse and one entry records, "* On one day, more than 40 carcasses of wildebeest were counted along the fence, and further west vultures could be seen circling everywhere." (Anonymous, 1963).

At this time the seriously overgrazed conditions around Kingfisherspruit gave rise to thoughts of artificially reducing the numbers of game in the area, particularly by the large-scale capture and translocation of wildebeest to the area north of the Letaba River which was regarded as understocked (Anonymous, 1963). However, these considerations never came to fruition.

During the winter months of 1963 the movements of the migratory herds "*... in the western boundary areas of the Tshokwane and Kingfisherspruit areas, were largely determined by the availability or of water in the winter grazing area", and could be characterised by restless shifting between artificial waterpoints and natural pans filled by occasional scattered showers which fell (Anonymous, 1963).

This again must be considered a manifestation of the disturbing effect that both the fence and the artificial water points had had on the sub-population. The fence, having excluded the Sand River as a water source, enforced the provision of artificial drinking sites and resulted initially in restless, unpredictable movements.

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* Translated from Afrikaans.

Between December 1963 and July 1965, Pienaar** (unpublished data) marked 121 wildebeest from seven localities in the CD. These were Lindanda - 41; Sabie River - 22; Kingfisherspruit - 12; Sweni - 4; Ngwenyene Dam - 10; Ripape/Hlangulene - 24; Mnondozi - 7; and Nwatindlopfu - 1. From these 121 animals, 322 resightings were recorded of which 34 (10,6%) had crossed the sub-population boundaries as we know them today. Of these, two crossed from sub-population three to two, five from one to two, eight from one to three and 19 from three to one respectively (Figure 3.1.2).

In retrospect, these data are difficult to interpret, but in comparison to the later marking program (this project), there would seem to have been a greater amount of crossing over of sub-population boundaries in the first by Pienaar's marked wildebeest than by those in this study. Of the 121 wildebeest marked in the first program, there were 34 subsequent records of marked animals having crossed such boundaries, while in this project (see Chapter 4) the respective figures were 6 out of 87 marked animals. Thus there was a significant difference (χ^2 = 9,19, $p < 0,01$) in the amount of movement across sub-population boundaries between the first marking program and the second which also reflects the turmoil caused by the fence and the enforced provision of artificial water points. Migratory herds, prevented from following their normal migratory patterns found themselves forced to seek summer grazing gounds elsewhere and crossed to and fro over the boundaries.

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* Translated from Afrikaans

** Pienaar, U. de V. Park Warden: Kruger National Park, Private Bag X402, Skukuza, 1350

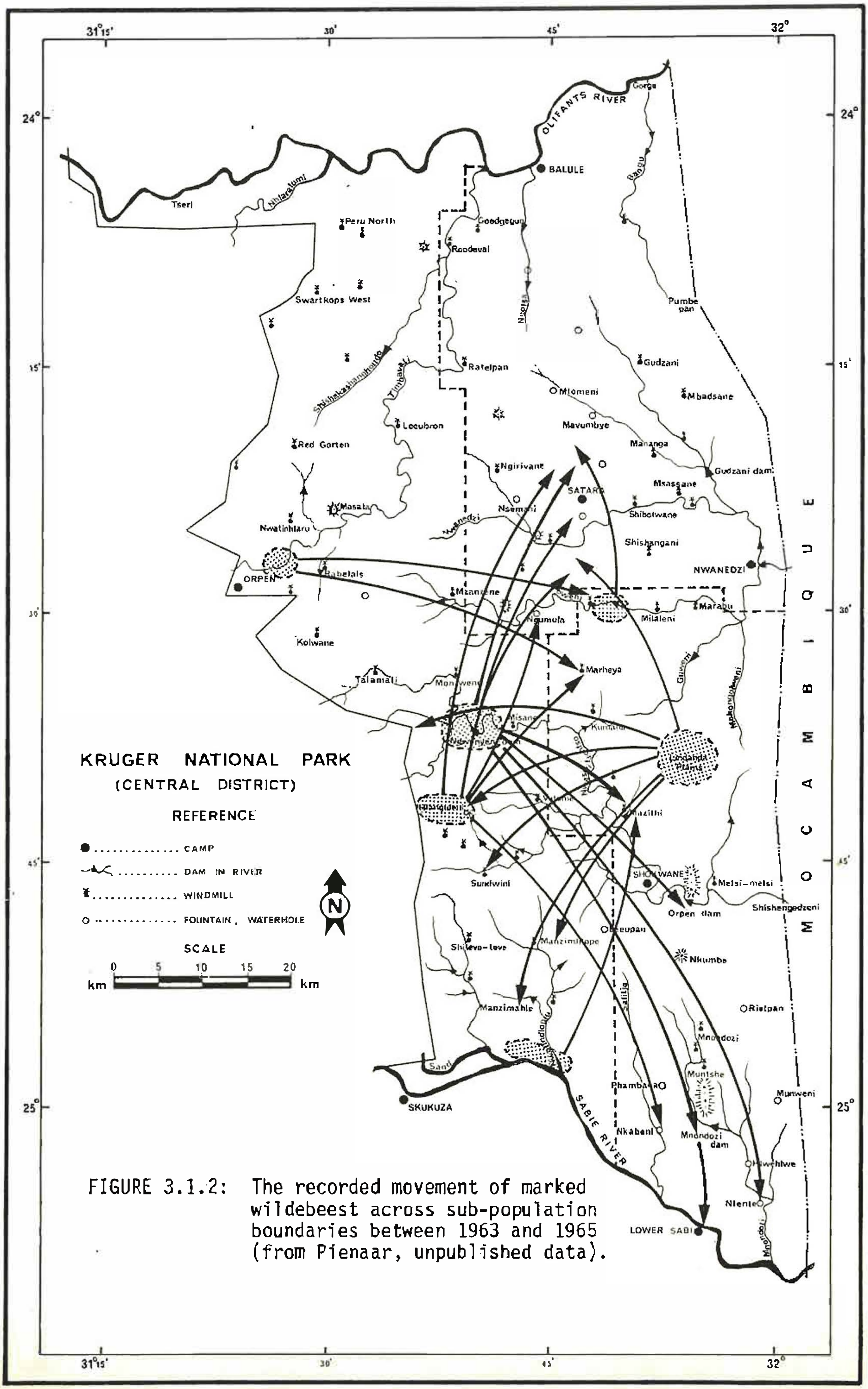

FIGURE 3.1.2: The recorded movement of marked wildebeest across sub-population boundaries between 1963 and 1965 (from Pienaar, unpublished data).

In 1965 (August) the first aerial census of wildebeest (and also of zebra and hippopotamus) was conducted. During this census 12 197 wildebeest were counted and localities of herds were carefully recorded (Pienaar, 1965) which proved of great subsequent value as individual herd totals could be allocated to the relevant sub-population allowing the calculation of sub-population totals.

The total of 12 197 must be regarded as an undercount. This count was undertaken during late winter months and flight routes were concentrated around areas where permanent water was available as it was supposed that this would be where wildebeest and zebra were most likely to be (Joubert, Pienaar, van Wyk and Smuts, 1974). Flight routes followed during this census are plotted in the report and it is clear that some fairly large and possibly important areas were not covered as intensively as others. It is also apparent from the flying times that this early census was not as comprehensive as the more modern ones; - a total of 19 hours 25 minutes were flown during 1965 while at present fixed wing surveys annually occupy a total of approximately 80 hours.

As the history of the population after 1965 is intimately connected to the trends as determined from subsequent population estimates, they are included here. They give the only reliable indication of population trend during the whole of the KNP's history as all previous reports of "increases" or "decreases" were subjective impressions of field staff. Data given here are from censuses up to 1984, and although this is far ahead of the period of the population's history at present under review, they are included at this point to facilitate further discussion.

In brief the trend was as follows. The population appeared to increase from 1965 to 1969 after which followed a 10-year period of decline. Thereafter followed a short but steep increase for three years up until 1982. The last two censuses recorded a slight decrease in 1983 and a similar increase in 1984. Table 3.1.1 presents these census totals, the type of census and the scource of the data, while Figure 3.1.3 illustrates the trend graphically.

Table 3.1.1: Annual estimates of the wildebeest population of the Central District of the Kruger National Park since 1965

YEAR	POPULATION ESTIMATE	TYPE OF CENSUS (See "Methods" - Chapt. 3)	SCOURCE OF DATA
1965	12 197	Helicopter	Pienaar (1965)
1966	No count	-	-
1967	No count	-	-
1968	13 130	Helicopter *	Pienaar (1968)
1969	13 950	Differential count	Pienaar (1969c)
1970	11 838	Helicopter *	Pienaar & Van Wyk (1970)
1971	10 650	Helicopter *	Joubert (1971)
1972	8 007	Helicopter & fixed wing**	Smuts & Pienaar (1972)
1973	7 700	Helicopter *	Joubert & Pienaar (1973)
1974	Count unreliable	-	Smuts (1975b)
1975	6 745	Helicopter *	Joubert & Pienaar (1975)
1976	5 783	Helicopter & fixed wing**	Joubert _et al._ (1976)
1977	4 569***	Helicopter	Joubert & Pienaar (1977)
1978	5 141	Ecological aerial surveys (E.A.S.)	Joubert (1978)
1979	4 768	E.A.S.	Joubert (1979)
1980	5 816	E.A.S.	Joubert (1980)
1981	6 512	E.A.S.	Joubert (1981)
1982	8 127	E.A.S.	Joubert (1982)
1983	7 584	E.A.S.	Joubert (1983c)
1984	8 026	E.A.S.	Joubert (1984)

* Helicopter count in conjunction with differential ground counts.

** A helicopter was used in wildebeest concentration areas while the 6-seater fixed wing was used in the more sparsely populated areas.

*** Count nowadays regarded as unreliably low.

Due to the severely trampled and overgrazed condition of the veld in the Orpen area, wildebeest culling was initiated in 1965. The program, which was to last for the next seven years (Table 3.1.2), eventually accounted for 3 155 animals of which 164 were culled during the first year.

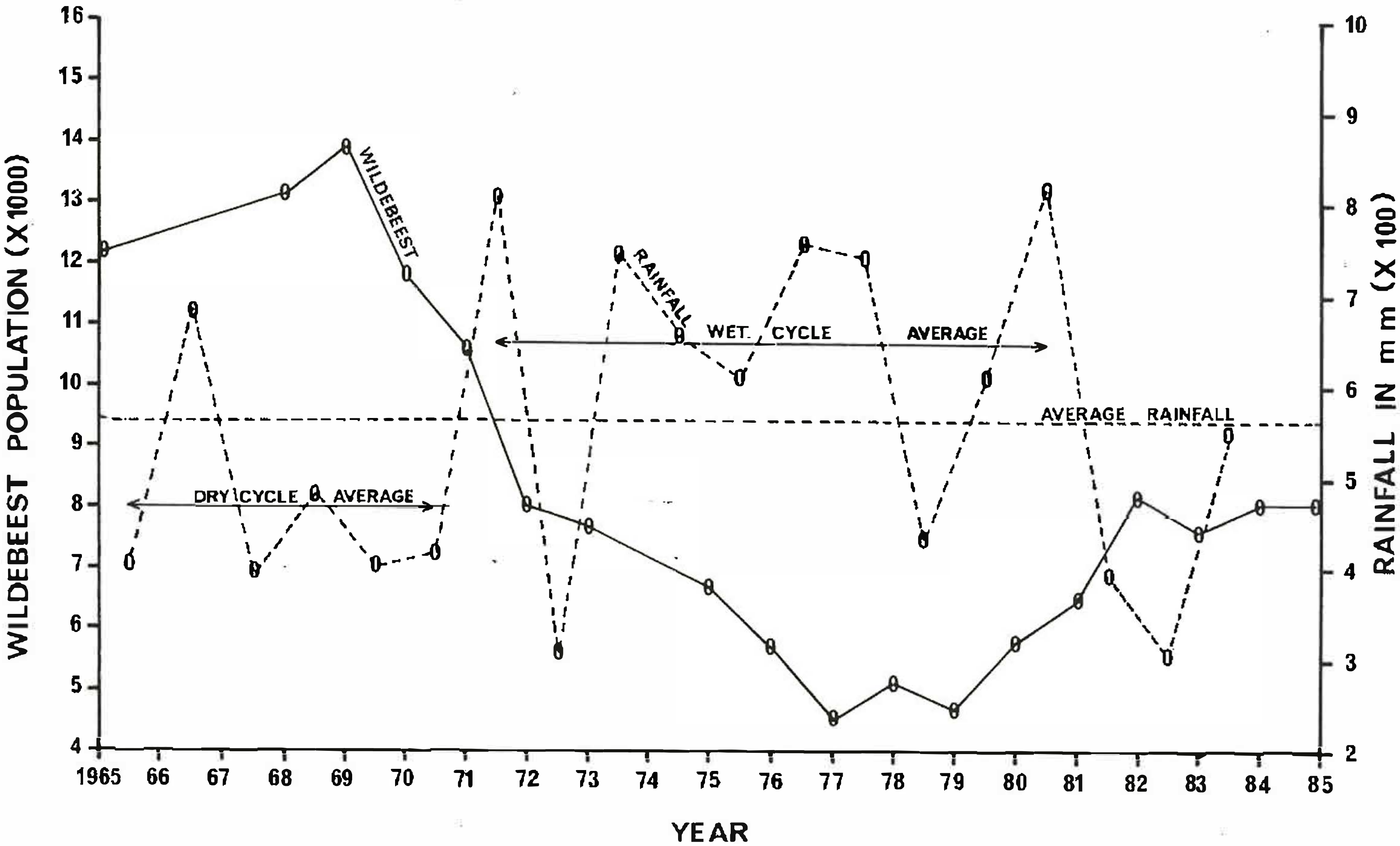

FIGURE 3.1.3: The trends of the wildebeest population of the Central District of the Kruger National Park since 1965. Rainfall is also shown.

Table 3.1.2: The number of wildebeest culled annually between the inception of culling in 1965 and its termination in 1971.

YEAR	NO. CULLED
1965	164
1966	392
1967	852
1968	368
1969	527
1970	550
1971	302
TOTAL	3 155

The overgrazed and trampled condition of the veld also led to the erection of a second game-proof fence from the Albatross Corner of the western boundary to the corner at Addger to keep the wildebeest and zebra herds off the overgrazed area and allow it a season or two to recover (see Figure 3.1.1). This fence was completed in August 1966 and stood until the beginning of the wet cycle (Gertenbach, 1980a) when the grazing had improved to the point where the exclusion of the migratory herds was no longer deemed necessary (Anonymous, 1972). Removal of the fence was completed in January 1972.

While in existence, this fence excluded virtually all of the *Chloris virgata/Acacia nigrescens* community of the "*Acacia* Veld on Gabbro" Landscape (Gertenbach, 1983a) from the wildebeest herds (refer to Figure 2.5.1 and Chapter 2, Section 2.5.11) which effectively denied them access to the traditional summer grazing areas - the western boundary fence having excluded some, and this second fence the rest.

Subsequent to 1964 and up to 1970, wildebeest received little attention in the annual reports (Anonymous, 1964; 1965; 1967; 1968; 1969; 1970) except that in 1969 the following significant report appears. "*It is clear that the Western Boundary migratory herds gathered in considerably smaller herds in the winter grazing area this winter. A large number of wildebeest apparently moved out of the old summer grazing area during the previous rainy season and crossed to the east to the Satara and Nwanedzi Sections where many of them spent the winter, particularly in the Bangu-Gudzane-area..... During the past rainy season, the remnants of Western Boundary herds also moved further north up the Kingfisherspruit game-proof fence as far as Chalons and Houtboschrand."

It seems clear that these abnormal movements were still as a result of the new fences and the wildebeests' attempts to find new summer grazing areas elsewhere and establish a new migratory pattern, and that now a thorough disruption of the ecology of this sub-population had occurred. In spite of this, censuses of the population of the CD indicated an increase between 1965 (Pienaar, 1965), 1968 (Pienaar, 1968) and 1969 (Anonymous, 1970) from 12 197 to 13 950. Should these figures have been accurate, this represents a 14,4% increase over the four year period. This is contrary to expectation as the disruption of the migratory system of the largest sub-population had occurred concomitantly with the culling programs, and in spite of this the population as a whole had continued to grow. This suggests one of two possibilities:

a) The population did in fact increase.

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* Translated from Afrikaans.

b) The population actually declined but population totals were derived from improved or different or incompatible census methods which implied an increase while the reverse was in fact in progress.

Either of these two alternatives seem possible. The years 1965 to 1969 were drier years (Gertenbach, 1980a) and these were known to favour wildebeest (Stevenson-Hamilton, 1939a). So although the migratory system had been disrupted and the summer grazing area excluded, the more favourable habitat conditions possibly prevailing as a result of drier conditions, may have permitted a population increase. It is also feasible that increases in the other two sub-populations masked the decline in the Western Boundary sub-population as sub-population totals were not calculated - the censuses arriving only at a single total for the population as a whole without particular regard for possible sub-population trends. (It must be remembered however that the sub-populations of the CD were only identified by later research (Smuts, 1972)).

On the other hand, census methods for the three counts differed. The count for 1965 was an aerial census by helicopter and the population total of 12 197 represents the actual number of wildebeest seen. As has already been said, some important areas may not have been covered as intensively as others which would have resulted in an under-count.

In 1968 wildebeest were also counted by helicopter, but this time the whole area of the CD was covered for the simultaneous census of elephant and buffalo. Actual flying time for the CD was not given but 97 hours were flown for the whole KNP. The CD comprises 28,4% of the KNP and therefore, if coverage of the CD continued at a similar rate as elsewhere in the KNP, flying time would have been in the order of 27,5 hours - an increase of 41,6% on the 19,4 hours of the 1965 census. Increased coverage of the area and longer flying time could be expected to result in an improved census total which for this census was 13 130.

The census of 1969 was delayed and therefore conducted later in the year than was desired (Pienaar 1969c). As a result, bad weather was experienced during most of the count and wildebeest could only be counted in the Kingfisherspruit area of the CD. Population totals were therefore derived from differential ground counts (see Section 4.2.2 for methods) and was thus a totally different method from the previous two occasions. This census estimated the population of the CD to be 13 950.

It is therefore easily conceivable that even though the population may have been declining (or static) the varying census techniques could have produced an illusion of population growth. Pienaar, in Joubert _et al_. (1974), was also of the opinion that the population had reached its peak in the early 1960's and had been declining since.

The aerial census of 1970 (Pienaar & van Wyk, 1970) recorded a decline in the population for the first time when the total was set at 11 838. This census followed the 1969 method and although it indicated a decline of 2 112 animals (15,1%) it did not at that stage evoke any concern, and culling continued.

In 1971, however, the decline had continued and the census total for the year was set at 10 650 (Joubert, 1971). This represented a further decline of 1 188 animals (10,0%) and culling was terminated immediately.

From this time on, subsequent aerial censuses revealed a continuing slide in the population until 1978 when, for the first time again, there was an apparent increase (Joubert, 1978; Joubert & Pienaar, 1973, 1975, 1977; Joubert, Pienaar & Kloppers, 1974; Joubert, Pienaar, Kloppers & Ackerman, 1976; Smuts & Pienaar, 1972). The lowest population total was recorded in 1977 when only 4 569 animals were counted and although this count is nowadays regarded to have been unreliably low (Joubert et al., 1974; Smuts, 1975b), it at the time represented a total decline of 9 381 wildebeest or 67,2% of the total population - an extremely worrying situation.

This concern led to the initiation of a two year study of the wildebeest population of the CD in 1971 (Braack, 1973). The objectives of this study were to obtain population statistics (from ground counts and a culled sample (n=78)) and to try to identify factors which may affect the dynamics of this species. Body growth was also described. Conclusions drawn from this study were that "bush encroachment" appeared to be diminishing the area of preferred natural habitat and that herds were being forced to occupy areas described as marginal for wildebeest and which greatly favoured predation.

The continuing decline in the population then led to the compilation of a comprehensive resumê of what was known about the zebra and wildebeest of the CD (Joubert et al., 1974). Speculative reasons for the decline were discussed and the following was concluded. "The extremely wet conditions experienced during the summer of 1971/72 had a deleterious effect on both zebra and wildebeest. During these months the tremendous increase in grass cover favoured the hunting activities of predators and caused zebra and wildebeest to concentrate on small areas where they were able to keep the grass short - during normal summers (grass growth not excessive) zebra and wildebeest are more dispersed and predators less successful in catching both young and adult animals. Counts undertaken during the summer of 1971/72 to register calving and foaling success, indicate that although above average crops were expected, they never materialized - this being due to the unusually high calf and foal mortality." In this report it was also recognised that with the erection of the western boundary fence a completely new "ecological adaptation would have to be made" by this population, but there was no mention made of the possibility that the disruption of the original system could in itself be the major cause of the decline.

In this report also, Smuts set acceptable maximum and minimum population levels for both the zebra and wildebeest populations of the CD and these were 12 000 and 8 000 for each respectively, with the further recommendation that it should be attempted to stabilise both populations at 10 000. He also recommended that "where the population level drops below the pre-decided mean level, all controlled reduction must be terminated. Should this retrogression continue and the populations approach their minimum levels, predator control measures should be initiated, where they are the prime cause of the reduction. Should other factors (e.g. water shortage) be the prime cause of the reduced population level, every endeavor must be made to alleviate them".

As the 1973 census total had already dropped below 8 000 (7 700) lion and hyaena culling was recommended (Joubert et al., 1974) and initiated in December 1974. Over the next six years, 394 lions and 318 hyaenas were culled in selected areas (Smuts, 1978b and personal data). Tables 3.1.3 and 3.1.4 give the totals, localities and sexes and ages of culled lion and hyaena respectively.

Table 3.1.3.: Dates, numbers, localities, sexes and ages of lions culled in the Central District of the Kruger National Park for the purpose of relieving predator pressure on the wildebeest and zebra populations of the area.

Sub-pop. area*	Locality and date of cropping operation	Total	Adults			Sub-adults			Large cubs			Small cubs		
			♂	♀	?	♂	♀	?	♂	♀	?	♂	♀	?
1	Sweni-Lindanda (Dec. 1974-Jan. 1975)	64	5	17	0	18	7	0	3	2	0	0	5	7
1	Mlondozi-Rietpan (Dec. 1975-Oct. 1976)	35	5	12	0	3	0	0	0	0	0	7	8	0
3	Kingfisherspruit (Dec. 1976)	61	5	15	0	11	5	0	2	4	0	7	4	6
2	Bangu-Balule (June 1977)	2	0	1	0	0	1	0	0	0	0	0	0	0
2	Satara-Nwanedzi (June-July 1977)	84	7	28	0	22	13	0	0	1	0	2	1	10
1	Mlondozi-Rietpan (July-Aug. 1977)	17	5	5	0	3	3	0	0	0	0	0	1	0
1	Sweni-Lindanda (Sept-Oct. 1977)	21	4	1	0	8	8	0	0	0	0	0	0	0
1	Sweni-Lindanda (Dec. 1978)	52[x]	-	-	-	-	-	-	-	-	-	-	-	-
1	Mlondozi (July 1978)	4	1	1	0	1	1	0	0	0	0	0	0	0
1	Sweni-Lindanda (Dec. 1979-Jan 1980)	54	8	16	0	7	12	0	4	4	0	2	1	0
TOTALS **		394	40	96	0	73	50	0	9	11	0	18	20	25

* Area 1 = Sweni/Mlondozi sub-population area; Area 2 = Satara sub-population area; Area 3 = Western Boundary sub-population area.

x No further data available.

** A further 51 lions were culled during this period in selected areas of the CD for management reasons other than the relief of predator pressure on the wildebeest and zebra populations.

Table 3.1.4: Dates, numbers, localities, sexes and ages of hyaena culled in the Central District of the Kruger National Park for the purpose of relieving predator pressure on the wildebeest and zebra populations of the area.

Area*	Locality and dates of cropping operation	♂	♀	Cubs	Unknown+	Total
1	Sweni-Lindanda (Dec.1974-Jan.1975)	29	26	32	4	91
2	Satara-Nwanedzi (Jan.1975-Feb.1975)	23	42	36	26	127
3	Kingfisherspruit (Dec. 1976)	23	23	17	0	63
1	Sweni-Lindanda (Dec. 1978)	9	9	0	28	46
1	Sweni-Lindanda (Dec.1979-Jan.1980)	7	8	0	6	21
TOTAL**		91	108	85	64	348

* Area 1 = Sweni/Mlondozi sub-population area; Area 2 = Satara sub-population area; Area 3 = Western Boundary sub-population area.

\+ No further data available.

** A further 46 hyaena were culled during this period in selected areas of the CD for management reasons other than the relief of predator pressure on the wildebeest and zebra populations.

This predator culling was to be conducted on an experimental basis which initially took the form of lion and hyaena surveys, the removal of certain proportions of the existing populations and then monitoring the reaction of prides and clans in and immediately outside the culling areas (Smuts, 1978a). The response of the prey populations was only gauged from the population trend which was inferred from each year's census total.

With attention having fallen on lions and hyaenas, Smuts (1975b) examined what was known of the population history of these animals. He concluded that with the provision of artificial water-points, and the subsequent stabilization of sedentary prey species around these waterpoints, the lion population of the CD had "at least doubled during the past 50 years", and after an extensive census of all lion prides in the CD (Smuts, 1976a; Smuts, Whyte and Dearlove, 1977; 1978), he estimated that at least 13 new prides had been established since 1956. Of these 13, four were in the Western Boundary sub-population area while two and seven new prides were established in the respective areas of the Satara and Sweni/Mlondozi sub-populations. Smuts drew no conclusions from this other than that the increase in lions was the result of increases in prey biomass due to the provision of artificial water points. However, from monthly returns of lion kills found by field staff, he concluded that "from 1971 onwards there has been a gradual but clear increase in the preference rating for both wildebeest and zebra. The value for wildebeest has in fact almost doubled from 2,27 to 4,35 for 1974/75". This aspect will receive detailed attention in Chapter 5.

More specific management proposals were submitted the following year (Smuts, 1976b). These were:

a) Artificial watering points - that all artificial waterholes influencing wildebeest and zebra in the major summer grazing areas (of the Western Boundary sub-population) and the transition zone between summer and winter areas, be closed down or made inaccessible to game as soon as practically possible, but before the end of March 1977. These include: Red Gorten, Hartebeesfontein dam, Nwatinhlaru, Ngwamutsatsa, Rabelais dam, Talamati, Fairfield, Monzwene, Misane mond and the waterhole near Orpen Camp (overflow from camp).

b) Rotational burning program -

i) A triennial burning program be initiated in the major summer grazing area whereby the blocks are burnt alternately before and after spring rain.

ii) That none of the blocks in the transitional zone be burnt in the mid-summer i.e. only after rain.

iii) That blocks in the winter grazing area be burnt three or four yearly (depending on the number of blocks available), alternately in the mid-summer and after the first spring rain.

c) That consideration be given to a further relaxation of buffalo cropping operations in the major ranges of wildebeest and zebra in the Central District and that similar consideration be given to elephant.

d) Predator control - that at least 80% of the lions and spotted hyaenas be removed from the summer grazing area and that this low predator density be maintained during the summer until wildebeest and zebra populations have recovered.

e) General - that all the above programs be continued until their influence can be gauged with certainty.

Of these four main proposals, only two were ever instituted - the burning program (Gertenbach, pers. comm.*) and the predator control (Smuts, 1978b; Van Rooyen, 1976). The burning program was altered and implemented in accordance with the proposals up until 1980 when the whole burning policy of the KNP was revised (Gertenbach, 1980b), while only one predator cropping operation was undertaken in the summer grazing area

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* Gertenbach, W.P.D. Senior Reserach Officer, Private Bag X402, Skukuza, 1350.

(Kingfisherspruit) of the Western Boundary sub-population in December 1976 (See tables 1.2.2 and 1.2.3). None of the artificial water holes were closed down and buffalo and elephant cropping continued in the area.

The population declined to its lowest recorded level of 4 569 in 1977 though, as has been said earlier, this was probably an extreme undercount due to prevailing conditions during the census. The census of 1978 (Joubert, 1978) subsequently showed an increase in the population but this increase was probably only the impression left by the poor count from the previous year. It is probable that the actual population total in 1977 was higher than that in 1978 (but lower than the 1976 total) and that there had in fact thus been a further decline to the more accurate census total of 5 141 in 1978 (refer to Table 3.1.1 and Figure 3.1.3).

Although various ground counts aimed at the determination or monitoring of population structure were conducted between 1968 and 1978, they were conducted with basically different goals in mind. It was only from June 1977 onwards that these counts took the form of the ones that were used for the duration of this study. Smuts (1978b) summarised the data still available from these counts. Only the data from the last of these counts (January 1978) are directly comparable to those from this study and have therefore been included in the analysis in Chapter 4.

Although the data from these earlier counts will not receive further analysis they have been included here for the sake of comprehensiveness (Table 3.1.5).

In 1979, the nadir in the decline was finally reached and subsequent counts recorded increases in the population for the next few years. This period however, falls in the study period for this project and receives detailed attention in the subsequent chapters.

Table 3.1.5: Population data for wildebeest in the Central District collected between 1968 and 1978 (from Smuts, 1978b).

Date of count	Sample size	Calves		Yearlings		Adult males		Adult females		Cow-calf ratio	Adult sex ratio (M:F)	Locality
		No.	%	No.	%	No.	%	No.	%			
1968	6 085	-	-	-	-	1 662	27,3	4 423	72,7	-	1:2,7	Whole Central District
1972	1 174	-	-	-	-	369	31,4	805	68,6	-	1:2,2	Whole Central District
2-7 Jan 1975	929	233	25,1	143	15,4	116	12,5	437	47,0	100:53,3	1:3,8	Satara, Bangu, Kingfisherspruit
2-7 Jan 1975	708	198	28,0	84	11,9	-	-	-	-	-	-	Sweni-Lindanda
2-7 Jan 1975	1 637	431	26,3	227	13,9	-	-	-	-	-	-	Whole Central District
14 Jan 1976	451	144	31,9	75	16,6	-	-	-	-	-	-	Guweni dam area only
7-9 June 1977	918	192	20,9	67	7,3	172	18,7	487	53,1	100:39,4	1:2,8	Whole Central
29 Nov to 1 Dec 1977	589	116	19,7	42	7,1	152	25,8	279	47,4	100:41,6	1:1,8	Whole Central District
24-27 Jan 1978	912	257	28,2	97	10,6	153	16,8	405	44,4	100:63,5	1:2,7	Whole Central District

CHAPTER 4

POPULATION TRENDS AND STRUCTURE

4.1 INTRODUCTION

When predator cropping was initiated in 1974 in the summer grazing grounds of the Sweni/Mlondozi sub-population (Figure 4.1.1), it was necessary to try to assess the effect that this was having on the wildebeest population. In order to achieve maximum advantage for the newly-born wildebeest calves, lion and hyaena cropping was conducted annually during December and January which is the calving season of the wildebeest in the KNP. To assess the effect of the lion cropping, quarterly ground counts to determine and monitor the sex- and age-structure of the three sub-populations were conducted (see Figure 4.1.1). Data from these counts which are available for use in this presentation are from January 1978 to January 1984. Largely as a result of information gained during these counts, lion cropping was terminated in 1979, but as some interesting trends in the structure of the wildebeest population had become evident, these counts were continued and the results form the basis of this chapter.

4.2 METHODS

4.2.1 Marked animals and movement

Wildebeest were captured by means of drug darting for the purpose of fitting colour-coded collars. The dart projector used throughout the study was a 32 gauge Cap-chur powder projector (Palmer Chemical and Equipment Co. INC.) modified by Van Rooyen*. Modifications

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* Mr. G. van Rooyen, National Parks Board, Private Bag X402, Skukuza, 1350.

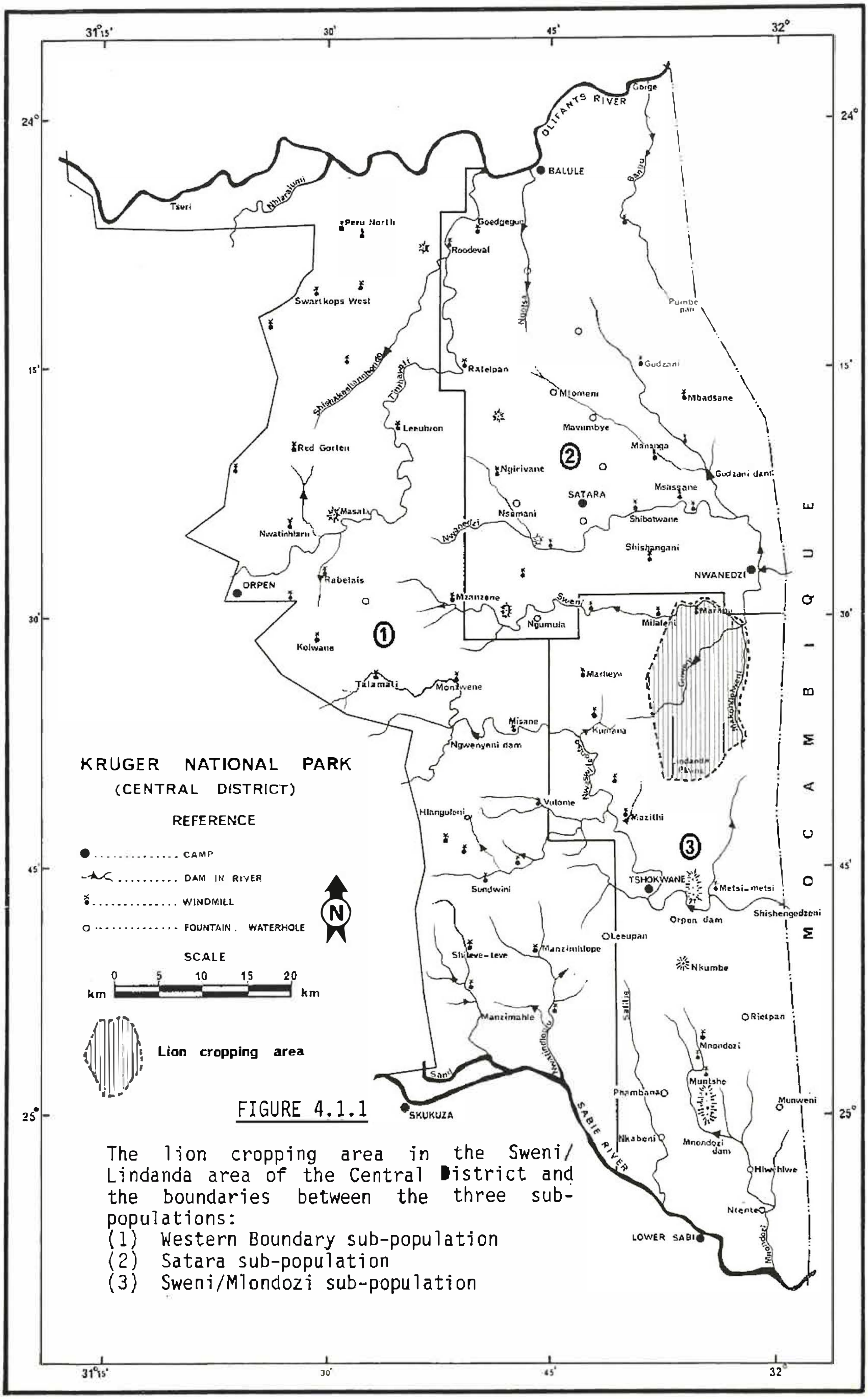

FIGURE 4.1.1

The lion cropping area in the Sweni/ Lindanda area of the Central District and the boundaries between the three sub-populations:

(1) Western Boundary sub-population
(2) Satara sub-population
(3) Sweni/Mlondozi sub-population

include an adjustable long/short range pressure adaptor and a more accurate hindsight calibrated for both long and short range.

Projectile syringes used were spring-loaded, barbless 1,1 ml capacity plastic darts developed by van Rooyen* similar to those described by De Vos et al. (1973). Barbless needles were selected as they drop out instantaneously thus minimising the irritation and alarm and reducing the flight distance of the animal after darting.

Fortunately most of the pioneer work on the development of chemical capture techniques has been done and today these procedures are straightforward. Recommended dosage rates (Pienaar, 1973a; de Vos 1977) give classic immobilisation reactions in wildebeest, and when used in conjunction with the sophisticated projectile syringes and projector mentioned above, wildebeest capture presents no problem.

In all cases wildebeest were darted from a vehicle. A herd would be approached obliquely and then circled, getting gradually closer. In this way alarm of the herd was reduced as the impression was given that the vehicle was driving past them and they would stand and watch. If the herd was approached directly, they would run off before an adequate darting distance of around 40 m was reached. A suitable adult animal, usually a cow, would be selected and darted.

An initial standard drug "cocktail" consisting of 3 mgm M99 (Etorphine hydrochloride, Reckitt & Sons) and 30 mgm Rompun (Xylazine hydrochloride, Bayer) was used on most of the captured wildebeest regardless of sex though only adult animals were selected. In some cases where darts were badly placed, boosters of varying dosages had to

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* Mr. G. van Rooyen, National Parks Board, Private Bag X402, Skukuza, 1350.

be administered. In the remainder of the wildebeest captured, a novel member of the Fentanyl family, Carfentanil (R 33799) (Janssen Pharmaceutica) was used. Carfentanil was administered at a dosage rate of 3 mgm either on its own or in conjunction with 30 mgm of Rompun.

At the report of the dart gun the herd usually ran only a short distance, the darted wildebeest tending to run a bit further, and if they were not disturbed again, would recommence grazing. The darted animal would usually return to the herd, calm down and collapse among them. The herd would then be slowly approached and the vehicle parked between them and the recumbent animal. This provided a visual screen and work could continue on the darted animal without unnecessarily alarming the rest of the herd. Age, according to incisor and canine eruption and wear after the method of Braack (1973), and sex were determined. This and other pertinent information was recorded on a proforma sheet (Figure 4.2.1) and the collar measured and fitted. (Horn dimensions were measured initially to assist in sex determination of found skulls, but sexual dimorphism is pronounced in horn characteristics and this proved unnecessary and was discontinued).

Wildebeest were marked using coloured collars similar to those used by Smuts (1972). It was obviously desirable that each collar (and thus each marked animal) should be individually recognisable (i.e. no two collars should bear the same mark) in order to prevent confusion as to the identity of the individual when resighted. Individuality was achieved by using striped collars in various colour combinations or different numbers, symbols or letters in various colours on a white background (Figure 4.2.2).

MARKED WILDEBEEST

No: 72 Sex: ♀ Age: 4 yrs Date: 83.02.11 Time: 14h45

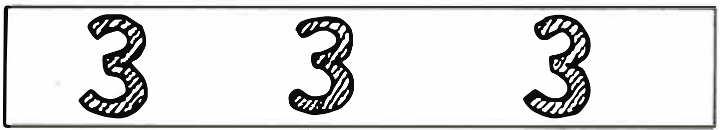
Accompanied by calf? Yes Pregnant: No Lactating: Yes

Locality where marked: Shitwembu Waterhole Grid ref.: 26.31 D

Cloud: 0/8 Temperature: Hot Humidity: Low

Structure of herd: Bulls: 1 Cows: 12 Calves: 8 Yearlings: 4

Collar used (Colours and symbols): Blue 3's on white



Dart used: Plastic with knobbed needle

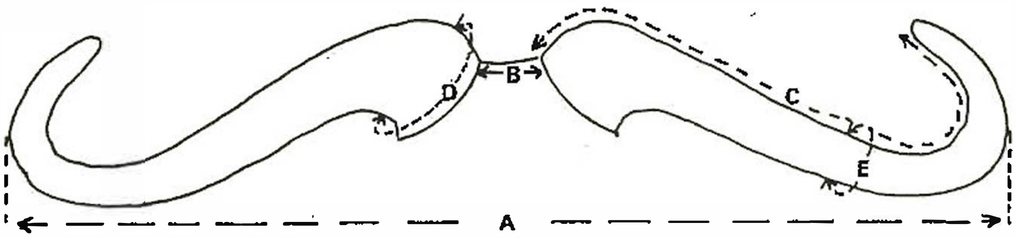
Drug used and dosages: M99 - 3 mgm; Rompun - 30 mgm

Darted at: 14 h 45 Goes down at 14 h 50 Induction time: 5 min

Distance run: ± 50 m

Antagonist: M5050 - 6 mgm Recovery: Very good

Horn measurements:



A: Not taken cms D: Not taken cms

B: " " cms E: " " cms

C: " " cms

Comments: Fully recovered within 20 minutes of being darted. Rejoins herd and her calf.

FIGURE 4.2.1: Example of proforma used to record information pertinent to wildebeest capture and marking.

FIGURE 4.2.2: Examples of colour codes and symbols on collars used to mark wildebeest.

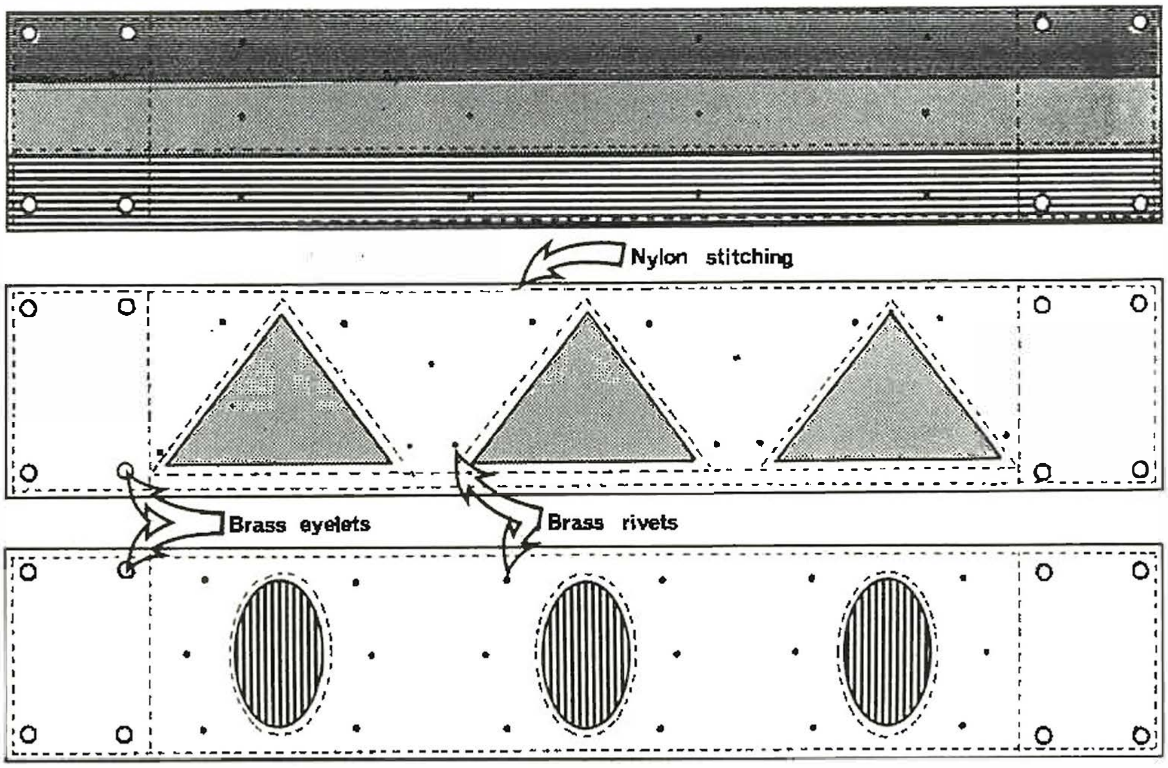
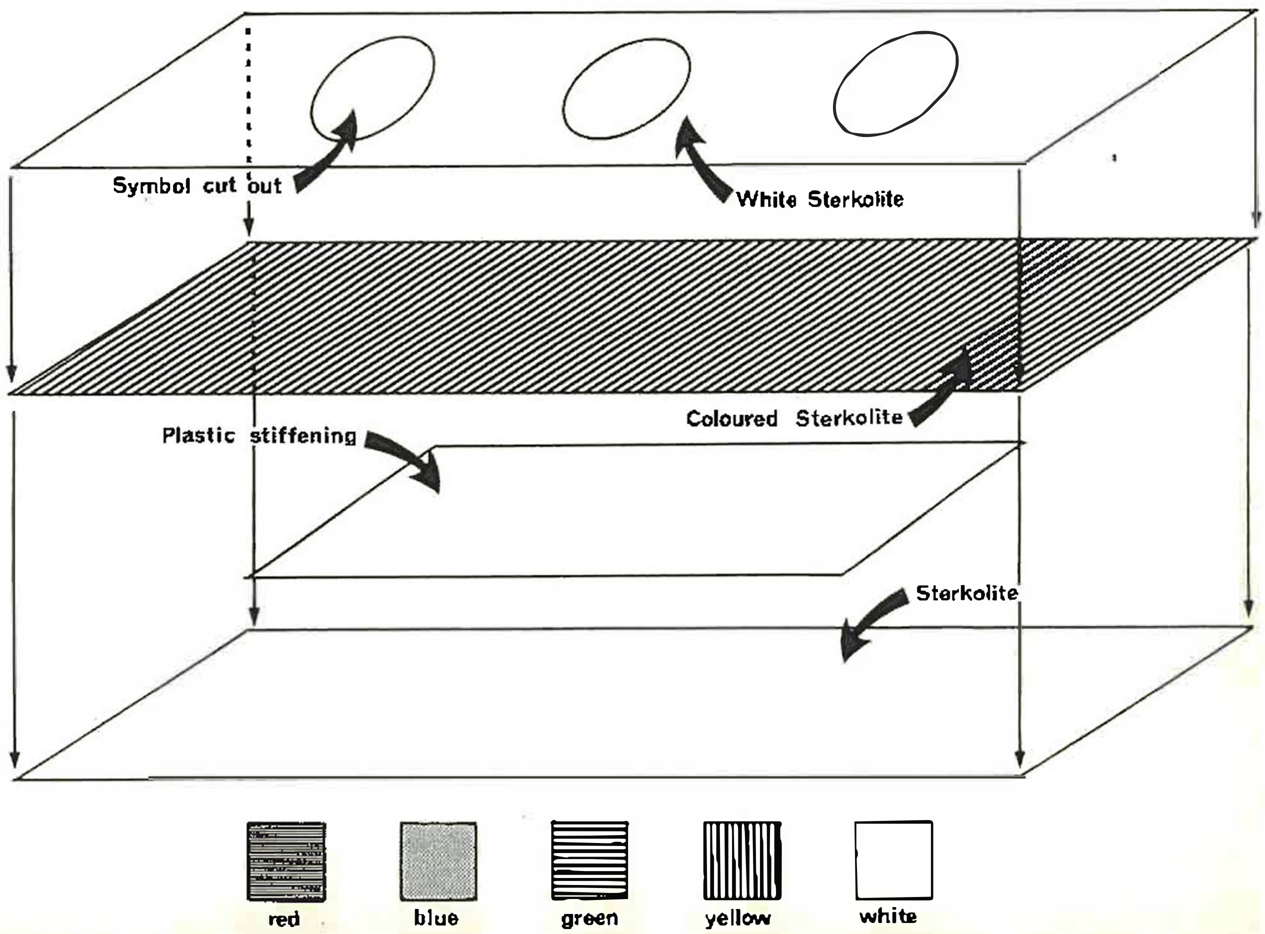


FIGURE 4.2.3: Showing the construction of the collars used to mark wildebeest.



"Sterkolite" (Kahn and Kahn), a commercially available polyvinyl plastic material impregnated and reinforced with nylon thread was used as it is manufactured in various colours. The material is also colourfast. Each collar was of the same basic construction - three layers of sterkolite with a strip of rigid plastic fitted between the second and third layers for additional reinforcement and to prevent the collar twisting (Figure 4.2.3). The layers were stitched together using nylon thread and further reinforced using brass split rivets fitted at strategic points. The collars were fitted on to the neck of the animals (Plate 4.2.1) by bolting the two ends of the collar together through brass sail eyelets (Cruiser Brand, size 26B). Eyelets were cut and mounted in the field after measuring the collar on the recumbent animal. This ensured a snug fit. Four steel bolts (25 mm X 10 mm) in conjunction with two galvanised body washers (diameter 25 mm) per bolt were used on each collar.

Brooks (1981) suggested that the use of machine belting instead of Sterkolite would significantly lengthen the life of the collar but for this study none of the suggested belting could be procured.

In all cases analgesia was reversed using M5050 (Diprenorphine hydrochloride, Reckitt & Sons) at dosage rates of 6 mgm for M99 and 9 mgm for Carfentanil. If there had not been too much disturbance during the operation, the marked animal could in most cases rejoin its original herd.

Resightings of animals were recorded during routine patrols by field staff, during quarterly ground counts of the wildebeest and during aerial surveys and censuses. Some resighting reports were received from tourists but these proved largely unreliable or gave insufficient information to be of use.

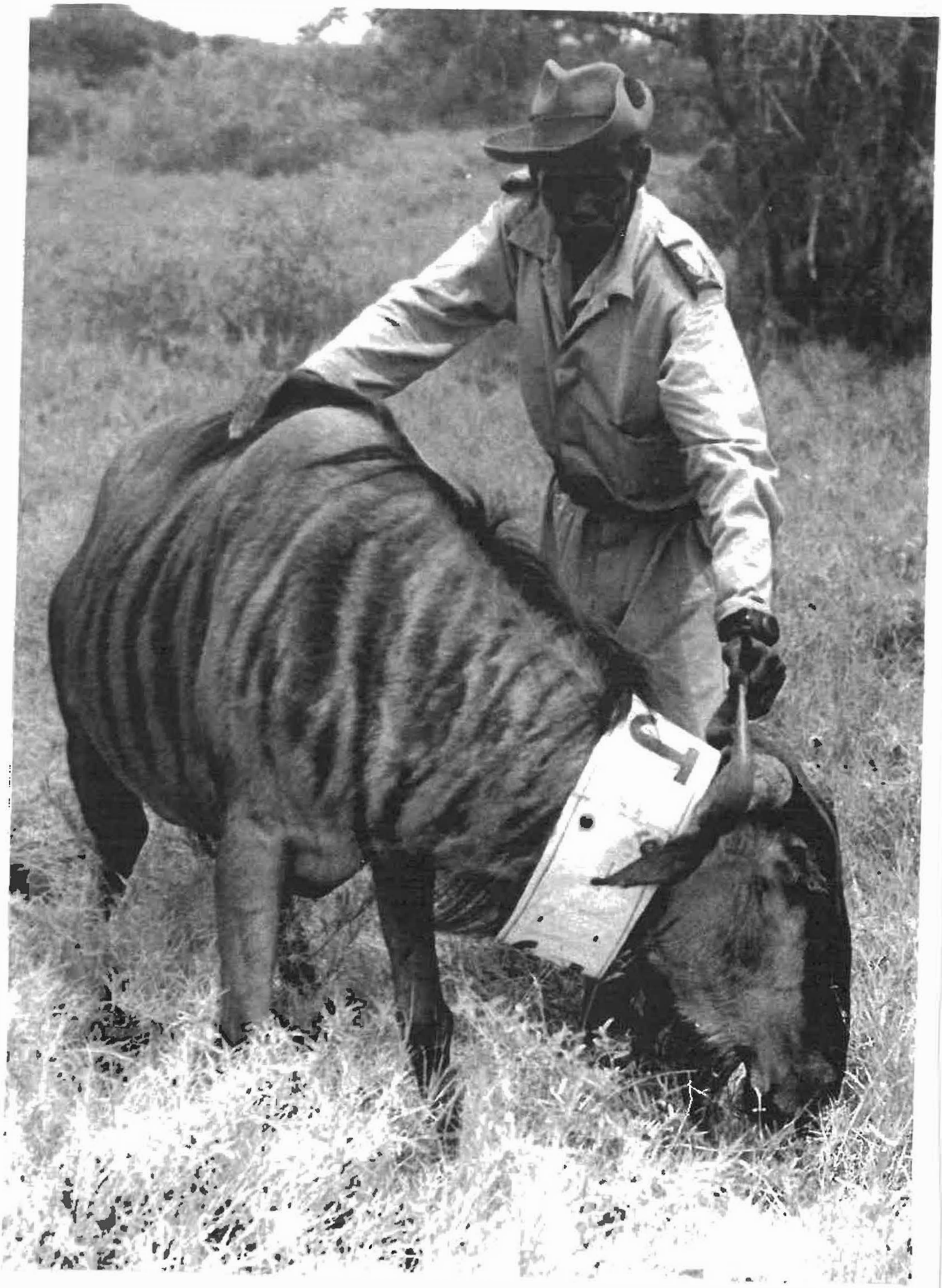


PLATE 4.2.1: An immobilised but not recumbent wildebeest cow marke[d] with a white collar with red "J"'s.

Initially information from Braack (1973) and Smuts (1972) were used to determine sub-population boundaries, and, as the objective of the marking programme was to confirm the movement patterns of this population and thus to assess the validity of the sub-population theory (Smuts, 1974b) and the analysis of sub-population data, the resightings of marked animals enabled the finer adjustment of these boundaries.

4.2.2 Population and sub-population trends

The monitoring of a species' population trends requires that accurate estimates of the population are obtained on a regular basis using a reliable and repeatable method. Since 1965 two basic methods have been used to census wildebeest in the KNP. These have been (a) helicopter counts which were either conducted as special wildebeest and zebra censuses or in which wildebeest were counted during buffalo and elephant censuses and (b) ecological aerial surveys by means of a fixed wing aircraft (Joubert, 1983b, in prep. b). Combinations of helicopter and fixed wing methods were also occasionally used. Population totals for the various years were derived as follows.

In 1965 the first aerial (helicopter) census was conducted on the wildebeest and zebra of the CD (Pienaar, 1965).

From 1968 onwards annual helicopter censuses of the elephant and buffalo populations of the whole KNP were done. In these counts routes were preplanned to obviate overlapping and thus double counting of herds. Flight routes covered the water complex of an area in its entirety (Pienaar, van Wyk & Fairall, 1966b). The procedure was to fly up one side of a major watercourse and then to branch off each of its tributaries and sub-tributaries in turn while those on the other side of the watercourse were covered on the return flight.

During the years 1968, 1969, 1970, 1971, 1973 and 1975 ground counts or "differential counts" were conducted simultaneously with the aerial census (Pienaar, 1968; 1969c; Pienaar & Van Wyk, 1970; Joubert, 1971; Joubert & Pienaar, 1973; 1975). These differential counts required that two other species (or "key species") be counted from the air, one of which was wildebeest. These differential counts were used to obtain population estimates of all other large mammal species and the method used was as follows. Flight and ground routes were planned prior to the census: flight routes were completed once only, while ground routes for each area were each repeated on five consecutive days. The totals obtained on the different ground routes of a section were pooled and the ratio of the different species in the count worked out accordingly. "Key species", were counted from the air in each section, one of which was always wildebeest. The calculation of the numbers of animals assumed the accuracy of the aerial census total of the key species. The calculation itself was simple: assume that 1 000 individuals of "key species" "A" (e.g. wildebeest) were counted from the air, and that species "A" constituted 10% of the total number of all the animals counted during the ground counts, then 10% = 1 000 individuals. If the species "B" (e.g. impala) made up 55% of all the animals counted on the ground then there would be $\frac{55}{1} \times \frac{1000}{10} = 5\ 500$ of species "B".

This method has obvious limitations and the results are probably largely unreliable when seen against those obtained by today's ecological aerial survey methods. Wildebeest however, was one of the key species and thus counted from the air and it can be assumed that even if the totals so obtained were not accurate estimates of the actual population size, at least the methods were repeatable and consistent and that the trends observed were reasonably accurate reflections of the actual population decline.

In 1972 concern over the continuing decline of the wildebeest and zebra populations prompted a special aerial census of these two species (Smuts and Pienaar, 1972). Both a helicopter and a six-seater fixed wing aircraft were used during this count - the helicopter being used to census areas with dense wildebeest and zebra concentrations and the fixed wing to cover the areas more sparsely populated.

In 1974 a special census of zebra and wildebeest was again conducted (Joubert, Pienaar, Van Wyk & Smuts, 1974) but owing to bad weather conditions and bad visibility due to lush summer conditions a very low count was obtained and is now considered to have been a gross underestimate (Smuts, 1975b).

In 1976 a special survey of the CD was again conducted using a helicopter and fixed wing aircraft (Joubert, Pienaar, Kloppers & Ackerman, 1976).

In 1977 there was no special census of the CD and therefore all the larger species were counted during the annual elephant and buffalo census conducted by helicopter (Joubert & Pienaar, 1977).

From 1978 onwards, population estimates have been obtained from the ecological aerial surveys which have been conducted annually between May and September (Joubert, 1978; 1979; 1980; 1981; 1982; 1983c). The methods employed are discussed in detail in Joubert (1983b; in prep. b). Of relevance here however is that all large mammals are counted and recorded in their precise location on suitable 1:100 000 maps. These maps are divided up into grids representing approximately 2 km X 2,5 km and all observations are fed into the computer which records them in their relevant grid square.

This grid system has divided the KNP up into 60 columns and 158 rows. Every second grid line between columns and rows in the system was numbered, the columns running from 01 in the west to 30 in the east. Rows were numbered from 01 in the south to 79 in the north. Each grid square in the system could therefore be allocated its own code. This was done as follows. The intersection point of each numbered north/south and east/west grid line received its number from the combination of its two grid lines, the north/south line's number followed by the east/west line's number. The four grid squares around this intersection point could therefore be individually recognised by the addition of a lettered code (A,B,C or D) behind the numbered code. Each grid square thus has a five digit code - four numbers and a letter which distinguishes it from any other grid square. As an example, Satara falls into the grid square coded 233DB. The CD lies between the 09 and the 30 north/south and the 40 and 11 east/west grid lines respectively.

The aerial surveys are so conducted that an attempt is made to count all animals of all species, but it is accepted that this is not achieved and that results do not represent actual population totals. Species vary considerably in their visibility and "countability" from the air and thus the proportions of the population actually seen and counted varies considerably from species to species. The method, however, has been standardised in such a way as to ensure repeatability (Joubert, 1983 b) and thus a relatively constant proportion of the population of each species is counted annually. Results can therefore be used to accurately assess the population trends.

Up to the present, no determination of actual population totals, standard deviations or confidence limits from the results has been attempted, but the Department of Statistics of the University of South Africa* is engaged in various projects concerned with the statistical analysis of the aerial survey data. Census results and experimentation have pointed to a high degree of repeatability (Joubert, 1983b).

Due to their dark colour, wildebeest are highly visible, and their choice of habitat (open plains) also renders them easily countable. Aerial survey counts are therefore regarded as closely reflecting the actual population totals of this species at the time of the survey.

Recent results of vegetation (Coetzee 1983; Gertenbach 1983a) and geological (Schutte, 1982; Dept. Research and Information, 1982a, 1982b) studies in conjunction with results from Smuts (1972) and Braack (1973) enabled an initial allocation of wildebeest sub-population boundaries. Resightings of marked wildebeest assisted in the refinement of these boundaries which were then incorporated into the aerial survey grid system in the computer. The computer can then extract the data per sub-population therefore making the assessment of sub-population totals and thus also trends possible (see Figure 4.1.1 (page 78) for sub-population boundaries).

The boundary between the Western Boundary sub-population and the other two was assigned roughly to the belt of Karoo sediments which in the CD runs from the Sabie River in the south to the Timbavati River in the north (see the simplified maps of the geology of the Central

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* Professor F. Lombard, Dept. of Statistics, UNISA, P.O. Box 392, Pretoria, 0001

District (Figure 2.3.2 on page 17) and Landscapes (Figure 2.5.1 on page 22). The boundary between the Satara and Sweni/Mlondozi sub-populations was set as closely as the grid system would allow along the Sweni River as only three marked animals of either sub-population were recorded crossing this river. See Appendix B for computer listing of the sub-population boundaries.

4.2.3 Population structure

Adult sex ratios and cow:calf ratios were determined by means of ground (vehicle) counts during which all individuals of all wildebeest herds encountered were classified according to sex and age. During these counts an attempt was made to cover as much of the CD as was feasible. Most of the different landscapes were sampled including those with high and low population densities. Each count took 4-5 days. Data on the distances covered per count are only available for nine counts (from old vehicle log sheets still available) and of these the average was 1 073,2 km (S.D. = 183,3 km). All other counts were conducted in the same way however. Both firebreak and tourist roads were covered and in order to ensure random sampling, all groups seen were sampled. Even if the herd was far off the road it was approached until close enough to identify age and sex classes.

If approached carefully wildebeest usually begin to move off slowly in file and this facilitated these counts to a large degree as each animal could be examined individually in turn. Each animal was classified by observing it through 8 X 40 binoculars and recording its age and/or sex on a tape recorder. The use of the tape recorder is considered to be essential as it obviated the need to observe and write up data simultaneously as the tape could be played back after each herd had been accurately classified, and the data then transcribed on to pro-forma sheets. Locality of each herd was also noted in order to allocate each herd to its relevant sub-population.

Counts were conducted quarterly, the first count in each year being done as soon after calving as possible. Survival rates of each calf crop could thus be monitored from birth to 21 months old. In total 23 counts were conducted, the first in January 1978 and the last in January 1984. For various reasons, two counts were missed, those being in July 1978 and July 1982.

On all counts an attempt was made to gain large sample sizes. Statistical procedures are available for the determination of the necessary sample size and confidence intervals from a given population size (Anonymous, 1977) and as far as possible it was attempted to exceed the required minima. Due to time and budgetary constraints however, this was not always possible.

In order to estimate the necessary sample size and confidence interval a technique of probability sampling of finite populations was used which necessitates some estimates and assumptions. These are:

a) The population must be clearly defined.

b) The sampling unit must be an animal which can be classified into distinct categories (e.g. adult bull, calf, yearling etc.).

c) An estimate of population size is required though the equations are not sensitive to error in the estimate.

d) The statistics used in the calculation incorporate the assumption of a normal distribution.

e) The assumption is made that the sampling design is random and unbiased.

For the wildebeest population of the CD, these assumptions can safely be made and the estimates of population size are obtained annually.

The necessary sample size can be estimated by the equation:

$$n = \frac{t^2aN}{\frac{100b^2N}{(a+100)^2} + t^2a}$$

where

n = required sample size (if a cow/calf ratio is required then n is the number of cows and calves which should be classified).

t = two-tailed "t" statistic (at the probability level of 90%, t = 1,645).

N = estimated total number in the population of the categories to be sampled (e.g. total number of cows + calves).

a = Estimated number of calves per 100 cows in the population.

b = Required precision (e.g. $\pm$ 5 calves per 100 cows).

After population ratio data were collected from ground counts, the confidence intervals were calculated on the sample size actually collected. This was according to an equation (Anonymous, 1977):

$$b \text{ (confidence interval)} = \frac{(a + 100)t}{10} \sqrt{a(\frac{1}{n} - \frac{1}{n})}$$

In order to keep the data simple and reliable only three age classes were used. These were calves (0-12 months), yearlings (13-24 months) and adult ($>$24 months). Attwell (1978) and Berry (1980a) included a fourth class (2-3 year olds) but I found field characteristics for cows in this age class to be unreliable particularly in the latter half of the year. This unreliability was further aggravated in large wildebeest concentrations where quick and reliable classification was imperative. As most of the cows in this age breed (100% of a sample of eight (Braack 1973)) these animals were considered to be adult. Bulls in this age class are more easily distinguishable but, as in the case with cows, they were classed as adults.

The following field characteristics were used for sex and age classification:

a) Calves: Owing to the strict seasonality of parturition the calf crop of any particular year is uniformly distinguishable. Animals in this age class are easily recognisable purely by size. Horn development is characteristic as is colour before the natal coat is lost at between 3 and 6 months of age. No sex differentiation is possible.

b) Yearlings: Yearlings are also readily distinguishable by size though this becomes less reliable towards the end of the second year. Slighter body build however, remains a highly reliable characteristic to an experienced observer. Horn growth characteristics are very reliable, the boss not having developed and being covered with hair. Sex differentiation is possible though difficult, and was not attempted as it was found to be unreliable if not impossible in larger milling herds.

c) Adults: Bulls are readily distinguishable from adult cows by larger body size, heavier boss and wider spread of the horns, black face and the angular appearance of the line of the belly when observed from the flank. This is caused by the penis shaft which extends anteriorly downward in a straight line to the centre of the belly. By contrast the belly of cow is more uniformly rounded. Sex of the animal was thus only recorded in this adult class.

4.3 RESULTS AND DISCUSSION

4.3.1 Marked animals and movement

In all, 87 wildebeest were marked at localities throughout the CD (Figure 4.3.1). An attempt was made to achieve a fairly even distribution of marked animals but in the larger concentrations (e.g. the Lindanda Plains) more animals were marked. As it was suspected that females were more mobile than territorial bulls, more cows were marked (57 cows : 30 bulls). Table 4.3.1 gives the numbers and sexes of wildebeest marked from the respective sub-populations.

Table 4.3.1: The number, sex and percentage of each sex of wildebeest marked in each sub-population of the Central District

Sex	Sweni/Mlondozi	Satara	Western Boundary	Total
Bulls Cows	18 (42,9%) 24 (57,1%)	7 (21,2%) 26 (78,8%)	5 (41,7%) 7 (58,3%)	30 (34,5%) 57 (65,5%)
Total	42	33	12	87

Of the 87 wildebeest captured, 77 were immobilised with the standard drug cocktail of 3 mgm M99 and 30 mgm Rompun. Of these, 55 had induction time and 64 had estimated flight distance from darting to

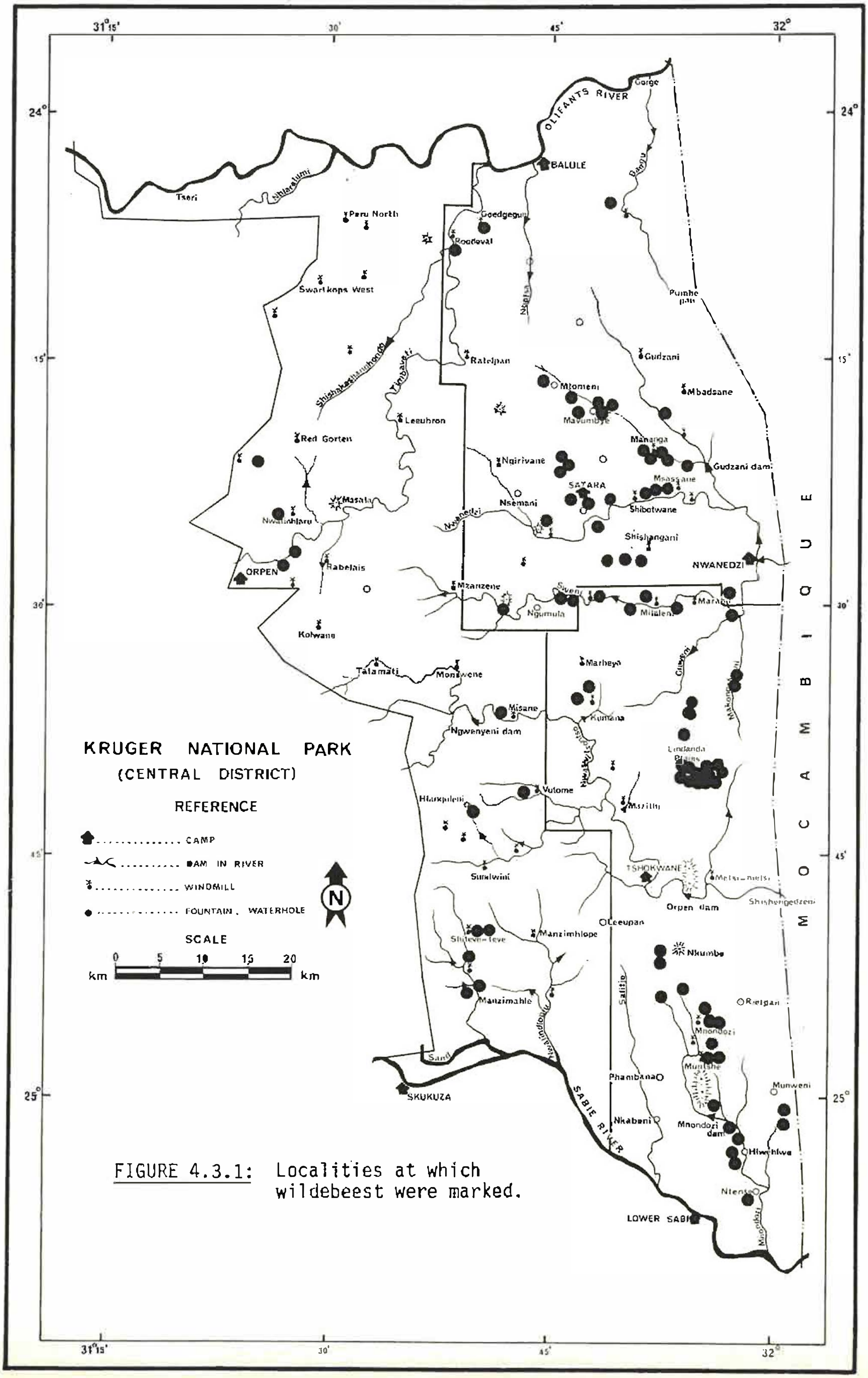

FIGURE 4.3.1: Localities at which wildebeest were marked.

recumbency recorded. The remaining 10 were immobilised with 3 mgm Carfentanil and 30 mgm Rompun of which nine had induction time and 10 had flight distance recorded. These data are summarised in Table 4.3.2.

Table 4.3.2: Induction time and estimated flight distance of wildebeest captured with M99 and Carfentanil in combination with Rompun

Drug cocktail	Induction time (min)				Estimated flight distance (m)			
	n	$\bar{x}$	Range	S.D.	n	$\bar{x}$	Range	S.D.
M99 + Rompun	55	5,75	2,0-20,0*	2,83	64	± 228	±50-1000	202
Carfentanil + Rompun	9	4,3	1,5- 6,5	1,46	10	± 280	±75- 500	205

* Adult bull tractable after 4 minutes but did not become recumbent (may not have received full drug dose).

Both of these drug combinations are highly effective in the capture of blue wildebeest. No excitement phase occurred during the induction phase which was quick and without complications. Five wildebeest were captured in conjunction with the marking programme for studies on the effects of drugs on various physiological parameters (Van Oewerkerk, in prep.). These animals, three cows and two bulls were captured with M99 and Rompun and were kept immobilised for an hour after induction for the collection of blood samples and other physiological data. Even though some of these animals were immobilised during the heat of middle day, no respiratory, cardiac or thermo-regulatory problems were encountered, and this cocktail is therefore considered to be the one of choice for wildebeest capture.

All captured wildebeest were resuscitated using the antidote M5050, Carfentanil requiring 9 mgm and M99 6 mgm for adequate reversal. Recovery of wildebeest captured using M99 was always effective and rapid while those captured with Carfentanil recovered much more slowly and were soporific and lethargic after rising to their feet. This residual effect could presumably lead to higher mortality of animals captured with Carfentanil. In this study however resightings were obtained of nine of the 10 (90%) animals immobilised with this drug, while 70 of the 77 (90,1%) of those captured with M99 were seen subsequently. Thus although the sample of animals immobilised with Carfentanil was small, there was no significant difference between the two drugs in terms of the proportions of animals resighted (and therefore also their subsequent survival) after capture.

In total there were resightings obtained of 79 of the 87 (90,8%) animals marked. There was thus a possible mortality rate of 9,2% of animals subsequent to capture. However, no evidence could be obtained to suggest that any of these animals had died as a result of the capture and marking operation. Only one old cow (15 years old) was subsequently found dead and she had been killed by lions 54 days after capture. One collar was also found that had been torn off the animal (an adult bull) and this was at a point 8 km from where he had been marked and 89 days later. One yearling was darted inadvertently and thus became separated from his mother and herd who had run off. When resuscitated, he ran around aimlessly searching for his herd, bawling all the time. This behaviour could easily have attracted predators and indeed he was not seen again. In two other cases (both adult bulls) the animals bolted after darting and could not be found. The chances were good that both of these animals would have died, but searches on subsequent days could reveal no trace of a carcass or attendant vultures. Thus in no case could any mortality be positively ascribed to the capture process. However, not seeing an animal subsequent to capture need obviously not mean that the animal had died. Collars could be torn off in territorial struggles or get snagged on branches and ripped off. The evidence shows that collars tend to be removed more easily by bulls than cows, which suggests that it is indeed in territorial skirmishes that this occurs. Mills* (pers. comm.) also found that wildebeest bulls in the Kalahari removed their collars more easily than cows. Of the eight animals marked and not resighted at all during this study, five (62,5%) were bulls. These five represent 16,7% of the 30 bulls that were marked while only three of the 57 cows (5,3%) were not seen again. This difference between the sexes was not significant (χ^2=1,85; $p>0,05$). However, only 12 of the 30 bulls were resighted for more than six months after marking while 40 of the 57 cows were still to be seen after the same period (χ^2=6,24; $p<0,05$).

Movements of marked animals confirmed the traditional movement patterns described by Braack (1973) and Smuts (1972) except that the migratory elements of the Western Boundary sub-population have died out (see also the section on sub-population trends, page 116), and the remnants of this sub-population are now completely sedentary.

The wildebeest of this sub-population were found to be confined largely to the "seep-lines" in the mixed Combretum/Terminalia sericea woodland landscape (see Figure 2.5.2) and the more open areas of the Acacia on gabbro landscape. Both of these landscapes provide patches of suitable open habitat (like islands in a sea) where the wildebeest can usually be found. These herds seldom leave these patches and apparently do so only to move to water or to go to another nearby patch. In the south of this area between the Nwanitsana Dam and Shiteve-teve windmill three fairly large seeplines occur which are interconnected by

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seepline "corridors" and in this area three bulls and two cows were marked. Resightings of these marked animals showed that they were largely confined to these three seeplines and corridors (Figure 3.3.2). Fifty eight resightings were obtained of these animals and in all except seven they were found on one or other of the seeplines. In the other seven cases they were found in the corridors en route from one to the other. The two marked cows were both seen on each of the three seeplines. The bulls were more territorial, each apparently having set up a territory on one of the seeplines upon which they usually could be found though there was some movement between seeplines. The bull marked at Shiteve-teve (No. 23) was seen twice at Timbetene and once on the corridor between the two while the bull marked at Timbetene (No. 22) was seen once at Nwanitsana.

The cows, calves and yearlings moved much more freely between these seeplines and could be encountered on any one of them. One cow, No. 18, was seen 28 times subsequent to marking of which eight were at Shiteve-teve, four were at Timbetene and 14 were at Nwanitsana. She was also seen twice on the corridor between Shiteve-teve and Timbetene (see Figure 4.3.2). There is also some evidence that these wildebeest move approximately 4 km to the east of Timbetene to another open patch on the gabbro soils (see Figure 2.5.1). After rains when the pans on this higher ground hold water the wildebeest disappear off the seeplines and on two occasions a herd was then seen on the gabbro soils to the east. These two observations were made from the air in the National Parks Board's aircraft and marked animals could not be distinguished but it was suspected that they were indeed the same animals. The degree of movement and number of sightings is given in Table 4.3.3.

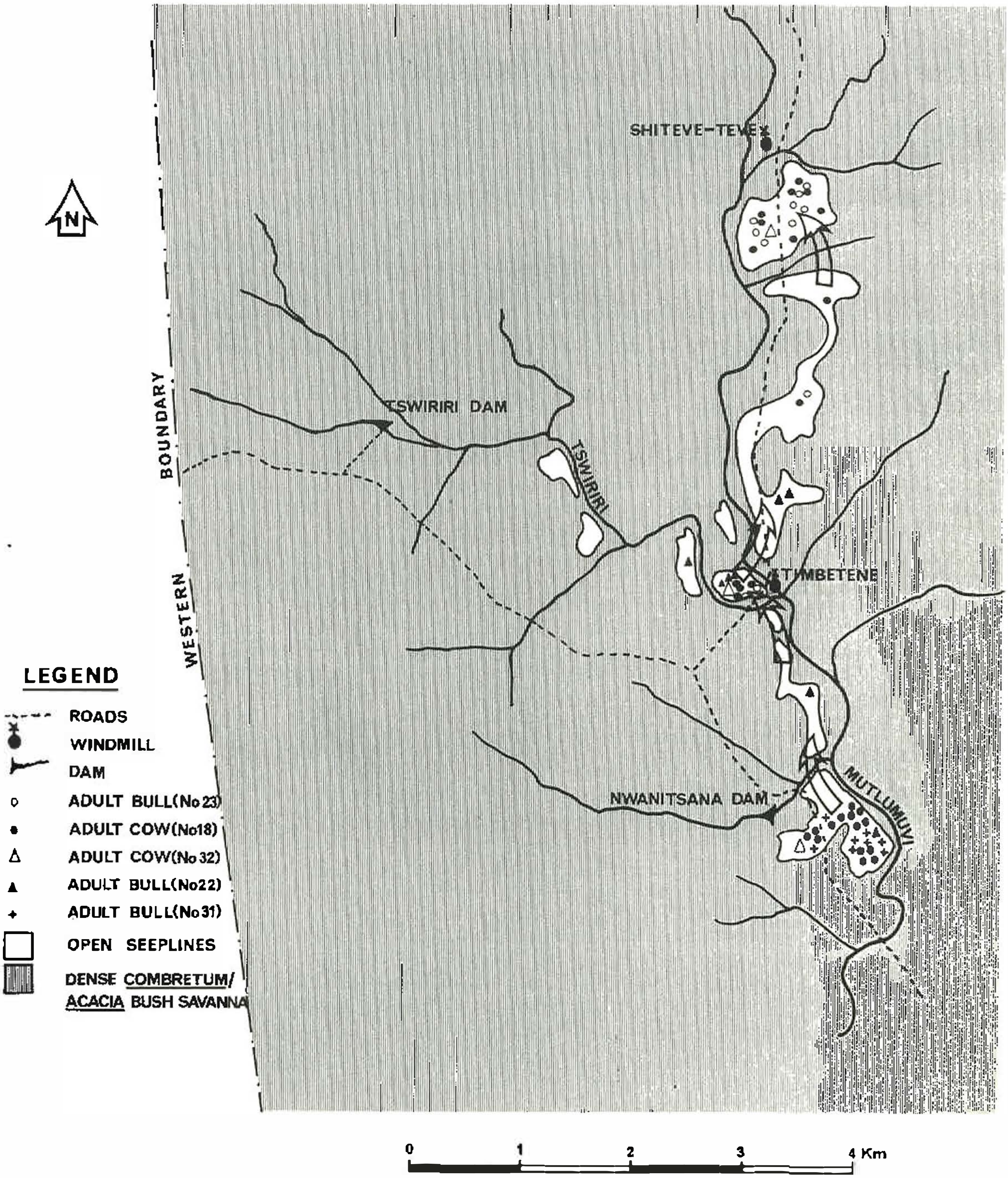


FIGURE 4.3.2: The movement patterns of the marked wildebeest in the Shiteve-teve area of the Western Boundary sub-population.

Table 4.3.3 Number of resightings and maximum distance between resightings and months between marking and last resighting of wildebeest marked in the Nwanitsana/Shiteve-teve area.

No. of marked animal	Sex	Date marked	Locality where marked	No. of resight-ings	Max. distance (km) between resightings	Months between marking & last sighting
18	F	27-01-81	Nwanitsana Dam	28	6,2	38
22	M	29-05-81	1 km North of Timbetene	8	3,15	10
23	M	29-05-81	Shiteve-teve	11	3,7	11
31	M	18-08-81	Nwanitsana Dam	8	0,75	6
32	F	18-09-81	Shiteve-teve	3	5,5	15

All other marked animals in this sub-population were also only seen at or very near their original marking site (Table 4.3.4).

Table 4.3.4 Number of resightings and maximum distance between sightings and months between marking and last resighting of wildebeest marked from the rest of the Western Boundary sub-population.

No. of marked animal	Sex	Date marked	Locality where marked	No. of resight-ings	Max. distance (km) between resightings	Months between marking & last sighting
24	F	09-07-81	Kingfisher-spruit	9*	3 km	6
25	F	09-07-81	Nwatinhlaru	5	1 km	6
26	F	09-07-81	Mhangadyana	4	3 km	9
27	M	09-07-81	Kingfisher-spruit	4	2 km	6
29	F	14-07-81	Misane windmill	2	0,5 km	1
30	F	21-07-81	Vutome Dam	6	3 km	9
58	M	10-02-83	Hlangulene	20**	0,5 km	11

* This cow was in a herd with another recognisable adult cow who had a naturally twisted horn. This disfigured cow was seen nine times subsequently in the same area, also with a maximum distance between sightings of for a period of 27 months between sightings. This suggests that the marked cow had either died or had removed its collar.

** This bull was seen almost daily by the attendants at the Hlangulene Picnic Place for the 11 months subsequent to marking.

Many of the other larger seeplines and more open gabbro areas in this Western Boundary sub-population appear to have attendant wildebeest herds as during ground counts, certain of these seeplines could be visited which would almost always have wildebeest on them (presumably the same herds) which also attests to the sedentary nature of this population. In particular these seeplines were those at Ngwenyene Dam, Orpen Gate, Misane Windmill, Ripape and Marumbene Dam.

In slight contrast to this sedentary pattern, the wildebeest of the Satara sub-population showed more movement, though such movement as was recorded, tended to be unpredictable and vagrant.

Of the 33 wildebeest marked in this area 12 were never recorded anywhere else but in the immediate vicinity of the marking site ($<$6,0 km), while nine more were only recorded at distances of less than 10 km. Six more moved up to 20 km while only three exceeded this distance (Table 4.3.5).

No clear pattern or migration could be discerned in these movements and at best could be related to availability of premium habitat conditions, which are variable in space and time depending primarily upon fire, rainfall and utilization. Apart from the more sedentary animals, the following movements were recorded (see also Figure 4.3.3).

Table 4.3.5: Number of sightings and maximum distance between sightings and months between marking and last resighting of wildebeest marked from the Satara sub-population.

No. of marked animal	Sex	Date marked	Locality where marked	No. of resightings	Max. distance (km) between resightings	Months between marking & last sighting
2	F	12-12-80	Nwanedzi Bridge	5	1	2
3	F	12-12-80	Sweni Firebreak	0	-	-
5	F	19-12-80	Nwanedzi River Road	15	10	25
7	F	20-12-80	Nwanedzi Plots	6	54	9
11	F	13-01-81	Shibotwane Windmill	11	8	10
12	F	13-01-81	Msassane Windmill	12	4	16
16	F	16-01-81	Goedgegun Windmill	16	20	22
17	F	16-01-81	Roodewal Windmill	5	2	24
19	F	29-01-81	Satara	16	7	12
20	M	29-01-81	Witpens Waterhole	0	-	-
28	F	21-07-81	Welverdiend Windmill	3	1	5
44	F	24-10-82	Nwanedzi Bridge	12	6	16
54	F	02-11-82	Nwanedzi Plots	6	13	22
55	F	03-11-82	Bangu Windmill	7	8	9
57*	F	19-01-82	Mlalene Windmill	5	10	13
59	M	10-02-83	Matikiti koppie	5	2	3
60	F	10-02-83	Satara	16	2	19
61	F	10-02-83	Muvumbye Windmill	15	5	12
62	F	10-02-83	Mtomene Windmill	2	5	4
63	M	10-02-83	Witpens trough	3	8	7
64	M	11-02-83	Witpens trough	6	20	17
65	F	11-02-83	Mavumbye Windmill	6	12	6
66	F	11-02-83	Mavumbye Windmill	5	23	13
67	M	11-02-83	Mananga Firebreak	3	8	1
68	F	11-02-83	Mananga Windmill	5	10	9
69	F	11-02-83	Mananga Windmill	5	2	9
70	F	11-02-83	Lewerik Windmill	7	15	19
71	F	11-02-83	Lewerik Windmill	3	9	9
72	F	11-02-83	Shikwembu Waterhole	3	1	9
73	F	11-02-83	Mbatsane Firebreak	0	-	-
74	F	11-02-83	Windmill	3	21	3
76	M	17-02-83	Sweni Windmill	4	9	7
77	F	17-02-83	Sweni Windmill	4	11	19
79	M	14-06-83	Shibotwane Windmill	16	1	12

* Although this cow was marked in the Sweni/Mlondozi sub-population area she is placed here due to her movements (see text).

In October 1980 the small block just to the west of Witpens waterhole was burned causing a concentration of zebra and wildebeest to build up. Marked animals which were attracted to the burn came from Mananga and even from further east down the Mavumbye spruit near Lewerik windmill. The high and sustained grazing pressure kept this block in a well-utilized condition - the grass being short and green with no build up of plant litter. These are ideal habitat conditions for wildebeest, the individual grass plants being maintained in a growing condition where protein content is high and structural tissue (cellulose) is minimal (Bell, 1971; Jarman, 1974). This condition has been maintained up to the time of writing though a more recent burn 3 km to the south west during June 1984 has induced most of the wildebeest and zebra away.

Other movements recorded are as follows: An old adult cow (No. 7) which was marked on a burn to the south of the Satara/Nwanedzi tarred road moved all the way down to Mlondozi Windmill. This was one of the few animals to have crossed the arbitrary boundary between the Satara and Sweni/Mlondozi sub-populations. She was almost definitely from the Sweni/Mlondozi sub-population and had crossed the boundary to utilize the burn, but then returned to the winter grazing area of that sub-population in the Mlondozi area.

An adult cow (No. 16) marked at Goedgegun windmill near Balule, moved twice to Ngotsa Dam and then back to Goedgegun, then down to Mtomene and was last seen at the Satara pipeline reservoirs. No explanation could be made for these movements except for the last which was on to a recent burn to the immediate south west of the Satara reservoirs (see Figure 4.3.3).

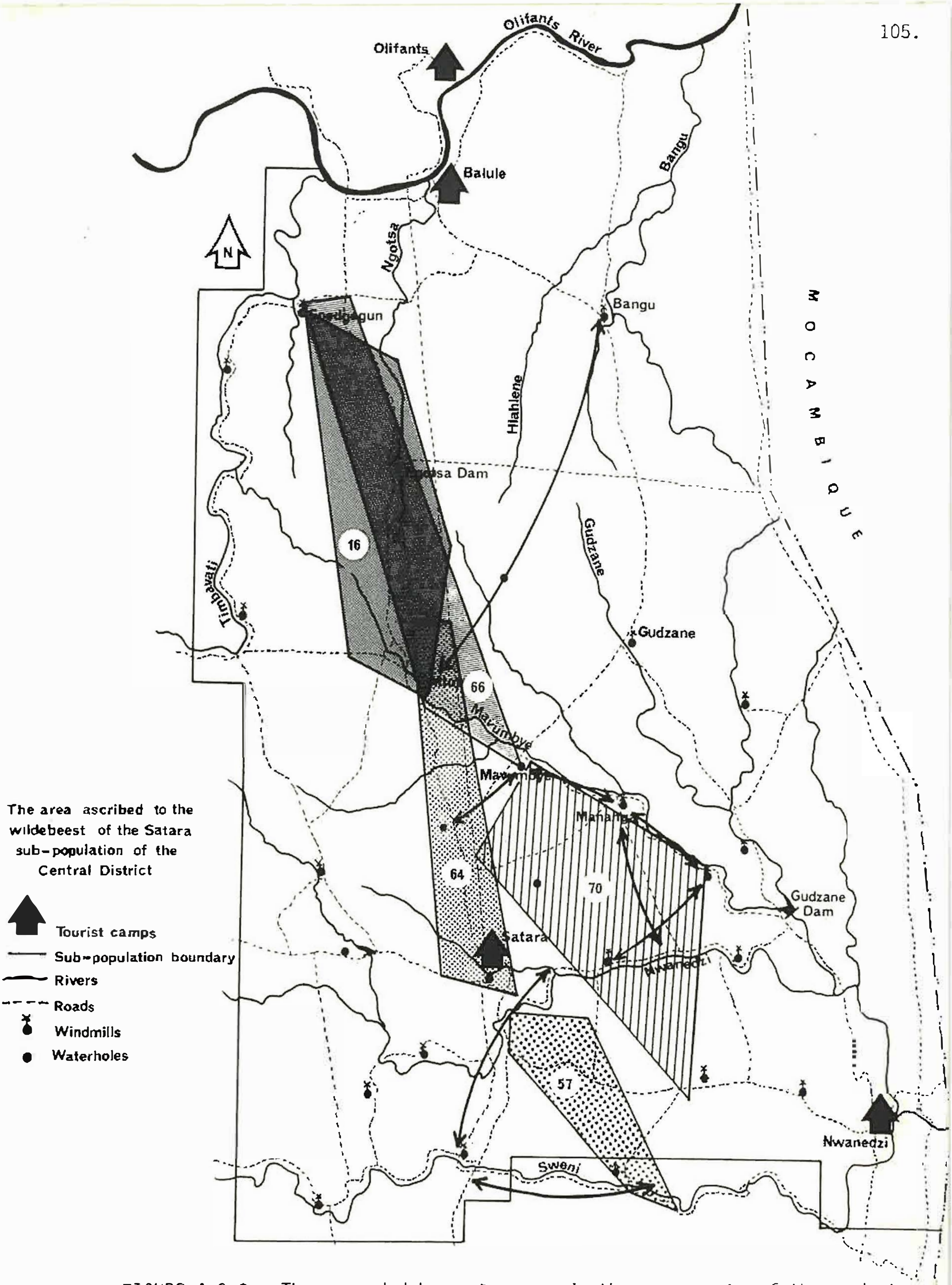


FIGURE 4.3.3: The recorded home ranges and other movements of the marked wildebeest of the Satara sub-population of the Central District of the Kruger National Park. Numbers indicate the number of the marked animal and shaded areas represent convex polygons connecting the outermost points of the nubmered animals observed home range. Arrows indicate movements of other marked wildebeest.

An adult cow (No. 54) which was marked on the Nwanedzi burning plots near Shishangaan Windmill moved steadily westwards and was last seen on the fresh burn to the north west of Satara in August 1984.

An adult cow (No. 57) moved from Mlalene Windmill where she was marked to the area around the Nwanedzi Bridge (where the main Skukuza/Satara tarred road crosses the Nwanedzi) and back again on two occasions. No reason for the moves was evident. This was also an animal that crossed the boundary between the Satara and the Sweni/Mlondozi sub-population. Although she was marked within the boundaries of the Sweni/Mlondozi sub-population whe was never recorded to have joined the southward migration and she was therefore placed in the Satara rather than the Sweni/Mlondozi sub-population (see Figure 4.3.3).

A three year old bull (No. 64) marked at Witpens trough moved south to Satara, then westwards towards Nsemane and then back northward to the Satara Pipeline Reservoir where he was last seen. None of these movements could be correlated to habitat conditions (see Figure 4.3.3).

An adult cow (No. 66) marked at Mavumbye windmill moved to Mtomene windmill and then northward to the junction of the Timbavati road with the main Satara/Letaba tarred road and west to Goedgegun windmill where she has been up to the time of writing. None of these movements could be explained (see Figure 4.3.3).

An adult cow (No. 70) which was marked between Mananga and Lewerik windmills moved south to the Nwanedzi burning plots near Shishangaan in the north west to Mavumbye. She retuned to the south-east as far as Shibotwane and was last seen on the powerline road 9 km north of Satara (see Figure 4.3.3).

An adult cow (No. 71) moved southwards from where she was marked near Lewerik windmill on the Mavumbye spruit to the Nwanedzi spruit. The field layer along the Mavumbye had become very rank as a result of good rainfall and apparently this had prompted a move to the more open brackish areas along the Nwanedzi.

An adult cow (No. 74) moved from Mtomene windmill to Bangu Windmill where she was last seen three months later. No reason for the move was evident.

A two year old bull (No. 76) moved eastwards down the Sweni spruit from the Sweni windmill to the Mlalene koppie. This was also one of the animals who crossed the sub-population boundary (see Figure 4.3.3).

Some of the bulls were completely sedentary and could be found on their territories at almost any time. One adult bull marked near Shibotwane on the Nwanedzi spruit (No. 79) and another marked at Matikite koppie also on the Nwanedzi spruit (No. 59) were never recorded anywhere else than their marking site.

In contrast to these two sub-populations, marked animals from the Sweni/Mlondozi sub-population (see Table 4.3.6 overleaf) nearly all showed movement patterns which conformed to these described for this sub-population by Smuts (1972) and Braack (1973). This entails a regular seasonal migration in which the winters are spent in the south of the range and the summers in the north.

Table 4.3.6: Number of sightings and maximum distance between sightings and months between marking and last resighting of wildebeest marked from the Sweni/Mlondozi sub-population.

No. of marked animal	Sex	Date marked	Locality where marked	No. of resightings	Max. distance (km) between resightings	Months between marking & last sighting
1	M	11-12-80	Mbhatsi turnoff	31	6	26
4	M	18-12-80	Guweni spruit	4	1	3
6	F	19-12-80	Lindanda Plots	3	2	1
8	F	29-12-80	Makonkolwene	7	29	39
9	F	30-12-80	Lindanda Plots	10	33	12
10	F	30-12-80	Mbhatsi turnoff	8	8	17
13	F	14-01-81	Makonkolweni drift	11	42	31
14	F	15-01-81	Lindanda Firebreak	10	48	22
15	F	15-01-81	Lindanda Plains	14	20	23
21	M	07-04-81	Lindanda Plains	9	1	3
33	F	28-09-82	Saalbek Windmill	5	30	12
34	F	28-09-82	Muntshe Windmill	2	4	10
35	M	28-09-82	Mlondozi Windmill	0	-	-
36	F	28-09-82	Nkumbe Firebreak	2	7	3
37	M	28-09-82	Ntente Waterhole	2	8	3
38	F	29-09-82	Hlwehlwe Waterhole	7	60	23
39	M	29-09-82	Mahlantswana spruit	2	41	4
40	M	29-09-82	Nkumbe koppie	2	1	1
41	F	29-09-82	Nkumbe koppie	2	1	1
42	F	05-10-82	Sweni spruit	12	11	18
43	M	21-10-82	Mlalene Windmill	10*	1	20
45	M	26-10-82	Saalbek Windmill	2	1	1
46	F	26-10-82	Oukraal Windmill	5	47	22
47	F	26-10-82	Muntshe	2	2	1
48	F	26-10-82	Muntshe Windmill	7	51	16
49	M	26-10-82	Mlondozi Windmill	0	-	-
50	F	26-10-82	Mlondozi Windmill	5	44	10
51	F	26-10-82	Mlondozi headwaters	2	7	10
52	F	26-10-82	Mahlantswana spruit	2	5	2
53	M	26-10-82	Hlwehlwe Waterhole	0	-	-
56	F	05-11-82	Kumana Dam	5	9	11
75	M	11-02-83	Kumana Dam	3	1	8
78	M	08-04-83	Lindanda Firebreak	8	1	7
80	M	06-10-83	Sweni flats	3	1	4
81	M	07-10-83	Sweni flats	2	1	1
82	F	24-02-84	Lindanda Plots	0	-	-
83	M	24-02-84	Lindanda Plots	4	2	2
84	F	24-02-84	Lindanda Plots	2	42	7
85	F	24-02-84	Lindanda Plots	2	2	2
86	M	24-02-84	Lindanda Plots	2	1	6
87	M	02-05-84	Lindanda Plots	0	-	-

* This bull was marked at my camp at Mlalene Windmill and could be found at will somewhere on his territory.

Wildebeest which produced the most information on movement were recorded to move as follows: An adult cow (No. 8) marked at Lindanda was seen again near Tshokwane, returned to Lindanda and was last seen at Guwene dam.

A yearling cow (No. 9) also marked at Lindanda moved south to Mlondozi where she was seen three times and then returned to Lindanda.

An adult cow (No. 13) marked at the eastern end of the Lindanda plots moved south to the Rietpan area then returned to area where she was marked. She was then seen in the south of her range about 4 km north east of Saalbek windmill. She then moved north west to a point about 7 km north of Valsdoring windmill, and was last seen back at Lindanda (see Figure 4.3.4(a)).

An adult cow (No. 14) migrated seasonally between the Marheya/Guwene area in the north and the Mlondozi/Rietpan area in the south for 22 months after marking (see Figure 4.3.4 (b)).

An adult cow (No. 38) marked near Saalbek windmill moved north to the Makonkolwene spruit and then returned to the Saalbek area. She then moved north again to Guwene Dam and was last seen a year later north of Tshokwane. She was in a long line of 25 wildebeest moving northward presumably after wintering in the south of the range where she had not been seen than winter (see Figure 4.3.4(b)). This cow was in a herd from which another cow (No. 46) was marked a month later. Subsequent to this these two cows were always recorded together on the five occasions that they were seen.

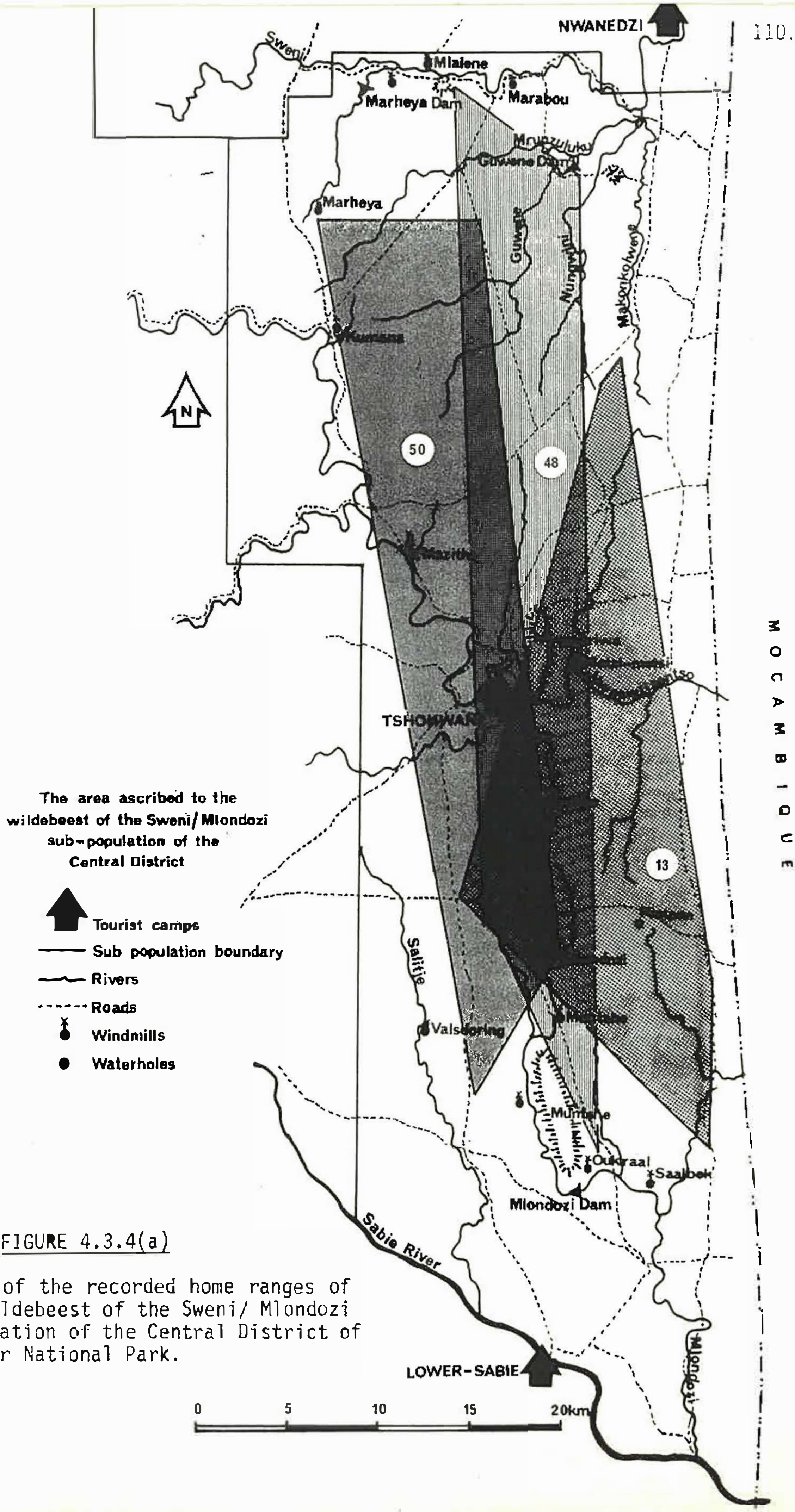


FIGURE 4.3.4(a)

Examples of the recorded home ranges of marked wildebeest of the Sweni/ Mlondozi sub-population of the Central District of the Kruger National Park.

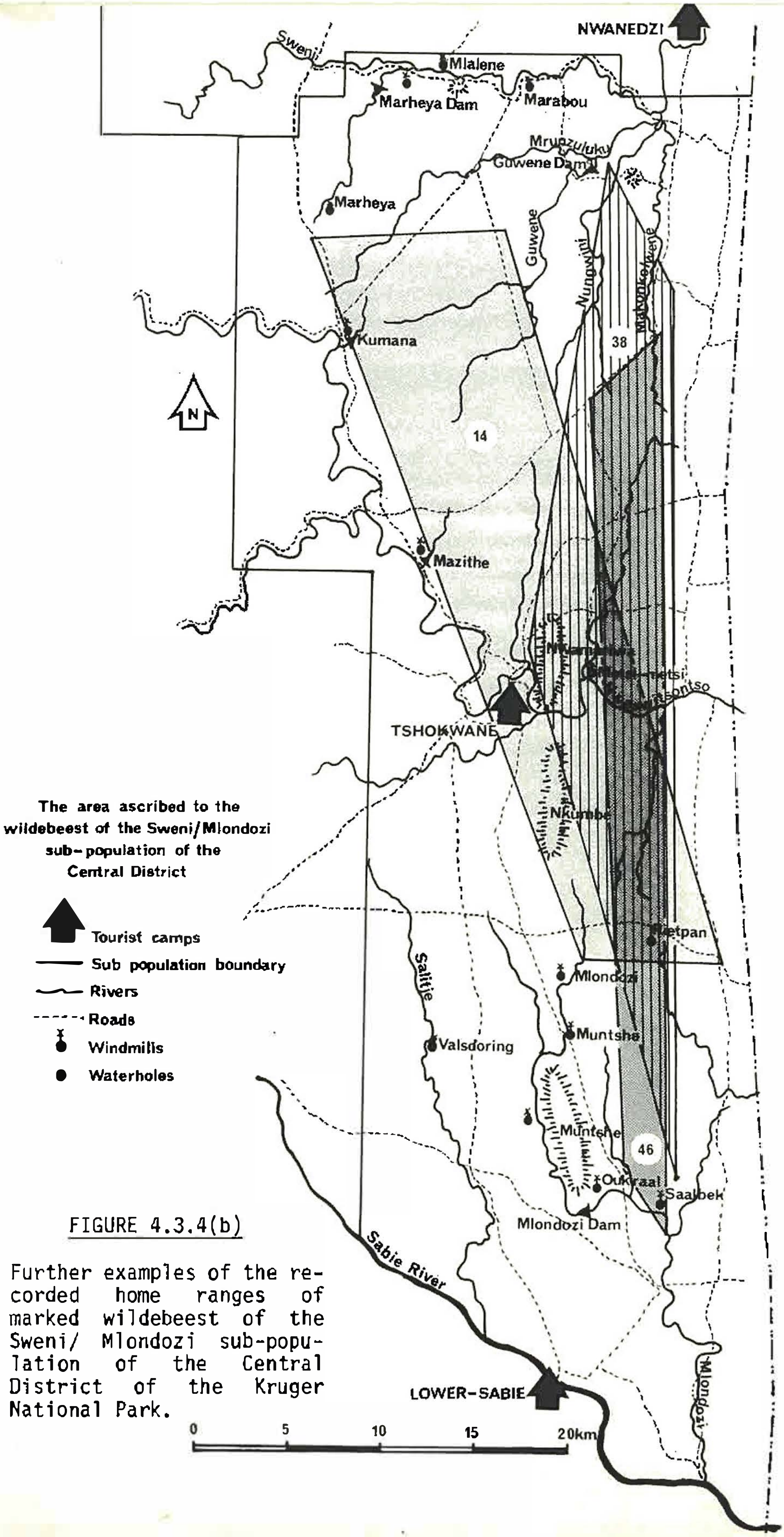


FIGURE 4.3.4(b)

Further examples of the recorded home ranges of marked wildebeest of the Sweni/ Mlondozi sub-population of the Central District of the Kruger National Park.

Another adult cow (No. 48) marked near Muntshe moved north to the Sweni spruit then south again to Oukraal windmill and then north again to Guwene Dam (Figure 4.3.4(a)).

An adult cow (No. 50) was marked at Mlondozi windmill after which she moved north nearly to Guwene dam. She then moved west and was recorded at Marheya windmill and then south again to the Klein Mlondozi spruit (Figure 4.3.4(a)).

Another adult cow (No. 84), marked at Lindanda, moved south to a point to the north-west of Saalbek and was then seen moving back northward again at Nkumbe.

All of the movements recorded above conformed exactly to the seasonal migratory pattern. Movements of other marked cows, while still conforming to this seasonal pattern, were not recorded over such wide distances. This was probably largely due to a lack of resightings at the extremeties of their range. Forty two marked animals from a population of about 3 000 (approximately 1,4%) is a small sample from a mobile group of animals and the small relative numbers of individual sightings reflect this. Significantly, of all the marked animals who were recorded to follow this migration only one was a bull (No. 39). This bull was marked in the winter in the southern part of the range of this sub-population at Mahlantswana and thus formed part of the migratory segment. He was solitary when marked but was with a breeding herd of 25 animals when he was seen again at Lindanda.

Of all the bulls marked in the northern part of the range (i.e. Lindanda and further north), none were recorded to move south with the migrants. These bulls include numbers 1, 4, 21, 75, 78, 80, 81, 83 and 86 (See Table 4.3.6). Although not many of these bulls retained their collars for long, none of these (with the exception of Nos 1 and 42 - see below) were recorded at distances of more than 2 km from their marking site. Bull No.1 was marked on the Makonkolwene River during December 1980 and between then and the end of April 1982 was subsequently seen 28 times within 1 km of his marking site. The pool at which he drank in the Makonkolwene River (on his territory) then dried up and he disappeared. He was then seen 6 km to the north five months later. However, once the rains came in January, he returned to his territory where he was seen twice during the following month. His collar was very tattered and worn by this time and although a bull was recorded on this territory subsequent to this it was not certain whether it was he who had lost his collar or whether he had been replaced by another bull.

The movement recorded by No. 42 was a west-east movement from the Sweni windmill eastward down the Sweni spruit and did not form part of the migration. This was also an animal which crossed the set boundaries from the Satara to the Sweni/ Mlondozi sub-population.

Thus it is clear that some of the bulls do not take part in the migration and stay behind on their territories in the northern part of the sub-population's range. This is the area where this sub-population spends the summer and it is here where calving as well as the mating, some 3,5 months later, takes place. It is thus here where the territorial activity is concentrated and it is obviously of importance to a bull to be already in possession of a territory when the migratory herds arrive. To achieve this, it is to a bull's distinct advantage to spend the period of the breeding animals' absence in defence of his territory even though it requires him spending this time in a solitary or semi-solitary state.

Conclusive evidence that this is the case comes from aerial survey data. During the annual aerial surveys the Sweni/Lindanda area is surveyed during June when the migrants of the sub-population are in the south of their range at Mlondozi. In order to get additional information on this area it was also surveyed in January of the years 1981-1984 when the migrant herds had returned. The data from these surveys are given in Table 4.3.7. As it is possible to distinguish adult territorial bulls from breeding herd animals from the air they were recorded separately as such during the surveys, making it possible to calculate ratios of bulls to breeding herd animals.

Table 4.3.7: The difference in the ratio of wildebeest bulls to wildebeest in breeding herds in the Sweni/Lindanda area in January and in June when the migratory herds are present and absent respectively.

YEAR	JANUARY				AUGUST			
	Bulls	Breeding herds	Breeding herd/Bull	Total	Bulls	Breeding herds	Breeding herd/Bull	Total
1981	135	1 721	12,7	1 856	149	1 389	9,3	1 539
1982	112	2 211	19,7	2 323	275	1 762	6,4	2 037
1983	102	1 178	11,5	1 280	188	1 350	7,2	1 538
1984	185	1 959	10,6	2 144	277	1 187	5,2	1 414
TOTAL	534	7 069	-	7 603	839	5 688	-	6 528
AVE.	133,5	1767,3	13,2	1900,8	209,8	1422,2	6,8	1632,0

As is clear from this table the proportion of animals in breeding herds per bull was always smaller in June. That is, there was a higher proportion of bulls in the area while the breeding migrants had moved south. By pooling the four January as well as June counts and testing the totals against one another (534 bulls to 7 069 breeding herd animals in January against 839 bulls to 5 688 breeding herd animals in June), a highly significant difference resulted (χ^2 = 135,4, P<0,001). This shows that a high proportion of bulls stays behind and the evidence from marked animals is that they do so on their established territories. Watson (1969) found that no bulls younger than 5 years were collected on territories and thus it seems possible that it is mainly the younger bulls which take part in the migration while the adult, territorial bulls remain on their territories.

From the recorded movement of these marked animals it is clear that basic differences exist between the three sub-populations. The Western Boundary sub-population at one time was the largest herd with a definite seasonal migratory pattern, but have now declined to a fraction of their former numbers and have become sedentary by nature (reasons for the decline will be discussed in the subsequent sections). The Satara sub-population are also mainly sedentary though showing some rather vagrant movements while the Sweni/Mlondozi sub-population have retained their traditional movement patterns which consist of a regular seasonal migration between the Sweni/Lindanda area in the north during the summer and the Mlondozi area in the south during the drier winter months.

These basic differences, in conjunction with the aerial survey system in which animal numbers and distributions are accurately plotted on maps, have enabled the analysis not only of population trends but of sub-population trends as well. This was done by the allocation of computer grid squares to specific sub-populations enabling computer-assisted extraction of sub-population sub-totals.

4.3.2 Population and sub-population trends

The history of the wildebeest population of the Central District has been covered in Chapter 3. This section will deal mainly with the recent history from January 1978 up to the time of writing but the period prior to this as far back as 1965 will also receive some attention. It was in January 1978 that wildebeest counts aimed at monitoring the effects of lion cropping were initiated. In brief and to recapitulate, the wildebeest population, subsequent to 1965 (when the first aerial census was conducted by Pienaar (1965)) apparently increased from 12 200 to about 14 000 after which a long decline occurred which brought the population to around 4 700 in 1979. From then on there was an increase in the population to around 8 100 in 1982 followed by a slight decline and then an increase in 1983 and 1984 respectively. Actual census figures were presented in Table 3.2.1 and were graphically depicted in Figure 3.1.3.

From these data it is possible to calculate rates of increase (or decrease) for the various increasing and declining parts of the population trend. Caughley (1977) defined several categories of rates of increase (r) but from these data only the "observed rate of increase" (r) can be calculated. This calculation carries no implication that either the rate of increase (or decrease) or the age distribution is constant over the period of observation. It is a general measure of the exponential rate at which a population increases over a period of time, and is calculated as the slope of a regression line fitted to data points representing the natural log of the population total plotted against time. The data used for these calculations are presented in Table 4.3.8.

Table 4.3.8: Rates of increase ($\bar{r}$) for the wildebeest population of the Central District of the Kruger National Park during increasing and declining phases of the population's trend*

YEAR	ASSIGNED TIME-SCALE VALUE	CENSUS TOTAL	LOG OF CENSUS TOTAL	POPULATION TREND	$\bar{r}$
65	1	12 197	9,4089	Increasing	0,0315
66	2	-	-		
67	3	-	-		
68	4	13 130	9,4827		
69	5	13 950	9,5432		
69	1	13 950	9,5432	Declining	-0,1043
70	2	11 838	9,3791		
71	3	10 650	9,2733		
72	4	8 007	8,9881		
73	5	7 700	8,9490		
74	6	- **	-		
75	7	6 745	8,8166		
76	8	5 783	8,6627		
77	9	- **	-		
78	10	5 141	8,5450		
79	11	4 768	8,4697		
79	1	4 768	8,4697	Increasing	0,1035
80	2	5 816	8,6684		
81	3	6 512	8,7814		
82	4	8 127	9,0029		
83	5	7 584	8,9338		
84	6	8 026	8,9904		

* These calculations assume the accuracy of the census totals.
** These not included in the calculation of $\bar{r}$ as they are considered unreliable.

Thus there was an apparent increase in the population of about 3% p.a. for the period 1965 to 1969 followed by an 11 year period of decline of about 10,4% p.a. This was followed by an increase of 17% p.a. for the next four years up to 1982 followed by a 2-year period of fluctuation. The rate of increase for the last six years was calculated for the period as a whole - ignoring the minor decline and subsequent increase in 1982 and 1983 respectively.

The reasons for these longer or shorter term fluctuations will be discussed later on in this chapter, but during the major decline, the population "crashed" from around an estimated total of 13 950 by 65,8% in a mere 10 years. Theories as to the reasons for the decline were put forward by some authors at the time (Smuts, 1975b; 1976b; 1978b; Joubert <u>et al.</u>, 1974) and these will be discussed later in this chapter.

One of the objectives of this project's marking programme was to confirm the "sub-population theory" (Smuts, 1972; Braack, 1973) and to assess the validity of assigning rigid areas to each respective sub-population which would enable analysis of sub-population trends. Of the 87 wildebeest marked only three were recorded to move over the ascribed boundaries. These were Nos. 7, 57 and 76. No. 7 was an adult cow who was marked just north of the Sweni River on a fresh burn. She subsequently moved south as far as Mlondozi Windmill, and must have been one of the Sweni/Mlondozi migrants who had crossed the Sweni River to utilize the fresh burn. No. 57 was an adult cow who was marked just south of the Sweni River but who was twice recorded to move northwestwards to the Nwanedzi spruit and back again. No. 76 was a two-year old bull who was marked on the Sweni just inside the Satara sub-population area. He subsequently moved eastward down the Sweni into the Sweni/Mlondozi sub-population area.

These minor movements over the boundaries lend support to the concept that the three sub-populations are relatively discrete and that separate analysis of sub-populations is valid. The issue is slightly clouded by the aerial survey data presented in Figure 4.3.5 and in Table 4.3.9 as the increases and declines of the Satara and Sweni/ Mlondozi sub-populations suggest that there was some movement across the boundaries in 1982, 1983 and 1984. The sudden increase in the Western Boundary sub-population in 1984 also suggests that some movement may have taken place across that boundary. By and large, however, the populations can be regarded as relatively discrete, but as the boundaries are not physical barriers some form of movement across them is to be expected.

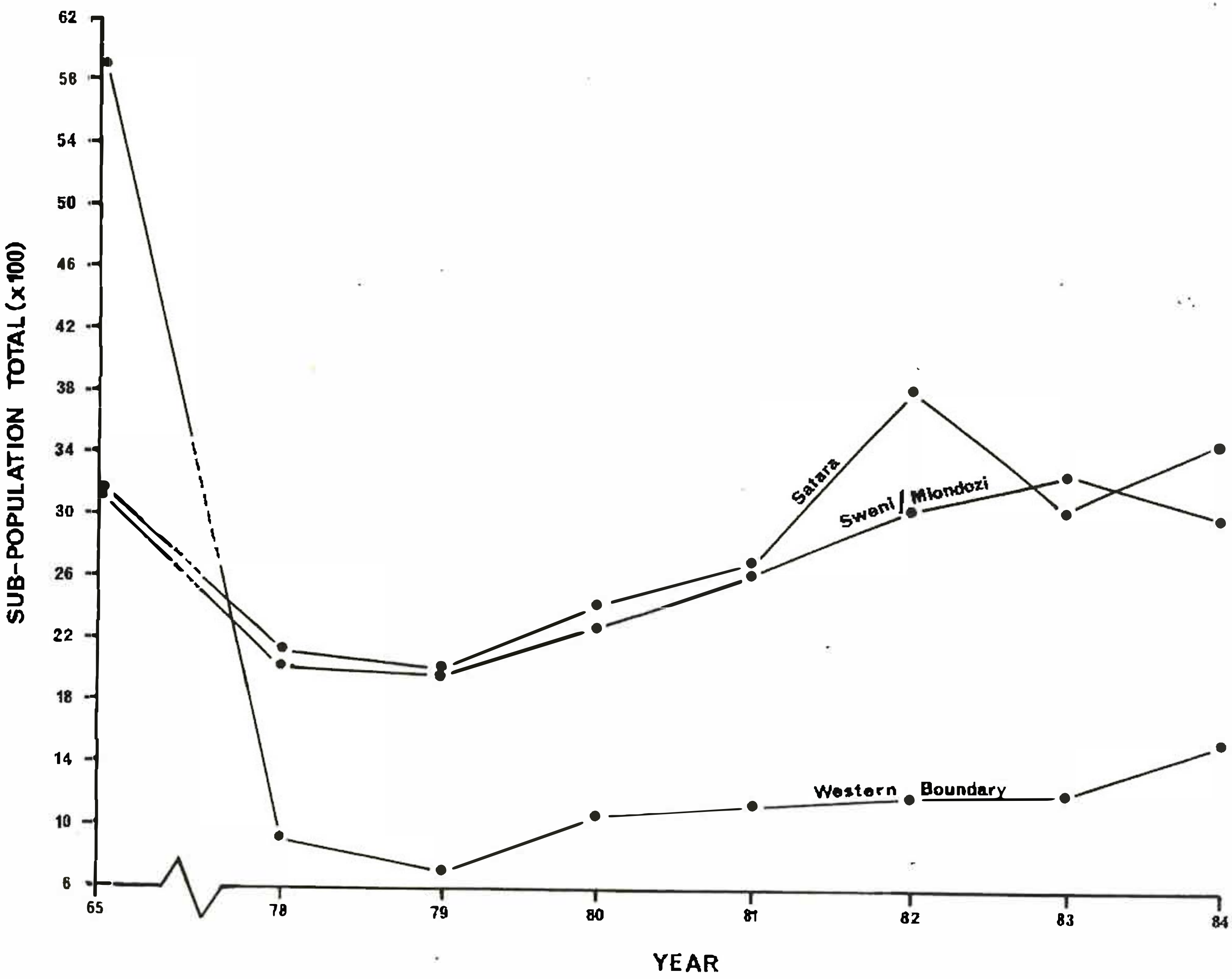


FIGURE 4.3.5: The trends in the sub-populations of blue wildebeest in the Central District of the Kruger National Park between 1965 and 1984.

Table 4.3.9: Trends in the wildebeest sub-populations of the Central District of the Kruger National Park between 1965 and 1984.

YEAR	SUB-POPULATION						TOTAL POPULATION	
	SWENI/MLONDOZI		SATARA		WEST. BOUNDARY			
	TOTAL	% DIFFERENCE	TOTAL	% DIFFERENCE	TOTAL	% DIFFERENCE	TOTAL	% DIFFERENCE
1965	3 134	-	3 149	-	5 914	-	12 197*	-
1978	2 021	- 35,5	2 161	- 31,4	959	- 83,8	5 141	- 57,9
1979	2 004	- 0,8	2 012	- 6,9	752	- 21,6	4 768	- 7,3
1980	2 298	+ 14,7	2 434	+ 21,0	1 084	+ 44,1	5 816	+ 22,0
1981	2 641	+ 14,9	2 712	+ 11,4	1 159	+ 6,9	6 512	+ 12,0
1982	3 078	+ 16,5	3 842	+ 41,7	1 207	+ 4,1	8 127	+ 24,8
1983	3 304	+ 7,3	3 061	- 20,3	1 219	+ 1,0	7 584	- 6,7
1984	2 995	- 9,4	3 464	+ 13,2	1 567	+ 28,5	8 026	+ 5,8

* This was not the highest recorded population level - it increased to 13 950 in 1969 for which year there is no distributional data to enable allocation to sub-populations. The decline of -57,9% therefore does not reflect the maximum recorded decline which should be 65,8%.

Pienaar (1965) reported on a helicopter census of zebra and wildebeest conducted during 1965. This was the first attempt at a comprehensive aerial census of these animals and his detailed report lists the totals and areas where herds were encountered. This enabled the allocation of the herds into the sub-populations as we know them today and they provide an extremely useful historical perspective into the decline and its causes. Pienaar's (1965) data and those from aerial surveys (Joubert, 1978; 1979; 1980; 1981; 1982; 1983(c); 1984) are presented in Table 4.3.10 and are also graphically shown in Figure 4.3.6.

These data show that although a decline occurred in all three of the sub-populatons, the major decline was recorded from the Western Boundary sub-population. The above table shows the decline between

1965 and 1978 and then annually thereafter. Table 4.3.10 shows the extent of the total decline between 1965 and 1979 when the lowest sub-population and population levels were recorded.

Table 4.3.10: The extent of the decline in the wildebeest population and sub-populations of the Central District of the Kruger National Park between 1965 and 1979

SUB-POPULATION	SUB-POPULATION TOTAL FROM PIENAAR (1965)	SUB-POPULATION TOTAL FROM JOUBERT (1979)	DIFFERENCE	% DECLINE
SWENI/MLONDOZI	3 134	2 004	1 130	- 36,1
SATARA	3 149	2 012	1 137	- 36,1
WESTERN BOUNDARY	5 914	752	5 162	- 87,3
TOTAL	12 197*	4 768	7 429	- 60,9

* See sub-script at the foot of the previous table.

It is of interest that the Sweni/Mlondozi and the Satara sub-populations showed an almost identical decline according to census totals. Also of interest is the much greater decline that was recorded in the Western Boundary sub-population. The "before" and "after" totals of the Western Boundary, when statistically tested against the pooled totals of the other two sub-populations, give a χ^2 value of 1538,6 an exceedingly high value which leaves no doubt that it was in this sub-population where the major decline occurred. The decline in this Western Boundary sub-population amounts to a classic population "crash" and the difference between this and the other two sub-populations suggests that some ecological factor or disturbance acted on this and not on the other two sub-populations. This factor was almost certainly the western boundary fences but this aspect will also receive attention under "Conclusions" later in this chapter.

It is also of interest to examine the contribution of each sub-population to the total decline (Table 4.3.11).

Table 4.3.11: The contribution of each wildebeest sub-population of the Central District of the Kruger National Park to the total decline of the whole population

SUB-POPULATION	SUB-POPULATION DECLINE	% OF TOTAL DECLINE
SWENI/MLONDOZI	1 130	15,2
SATARA	1 137	15,3
WESTERN BOUNDARY	5 162	69,5
TOTAL	7 429	100,0

Thus although the decline was highly significant, Table 4.3.11 and the previous table show that the vast majority thereof (nearly 70%) took place in only one sub-population and the decline is illustrated in Figure 4.3.6. This figure compares the distribution and density distribution of the wildebeest in the CD before and after the decline. Pienaar (1965) compiled a density distribution map after the census during that year and the map is reproduced here with his permission, while aerial survey data enabled the compilation of a similar map for 1979. Fortunately, both censuses were conducted in August when distribution patterns could be expected to be similar and the migratory herds should have been in the southern parts of their respective ranges. These two maps clearly show the disappearance of the migratory element of the Western Boundary sub-population.

The other two sub-populations also declined during the same period but only by a relatively small 36% each, and both have subsequently recovered to levels above those recorded in 1965. The Western Boundary sub-population has also recently shown an increasing trend but this may only be due to minor shifts over the sub-population boundaries.

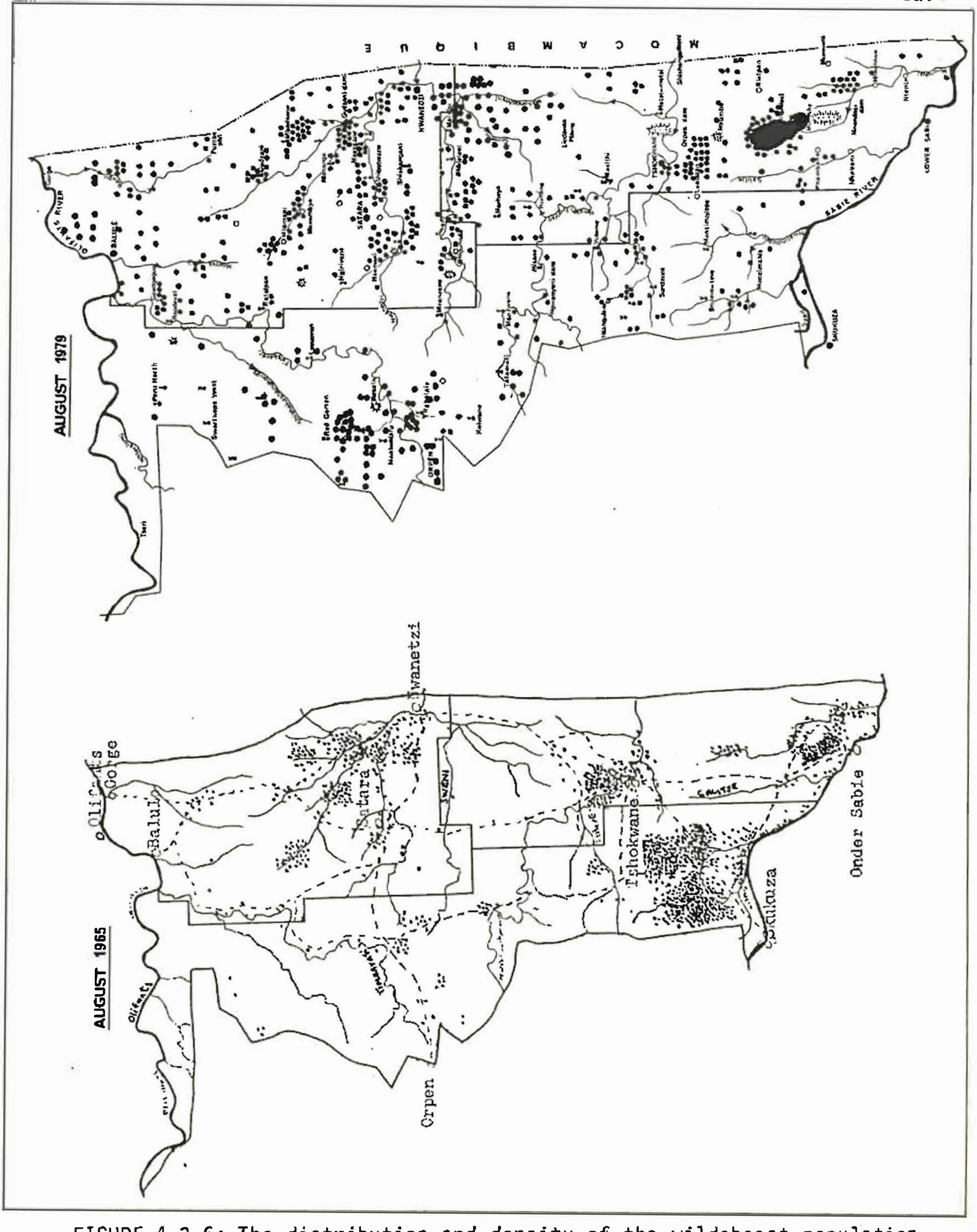


FIGURE 4.3.6: The distribution and density of the wildebeest population of the Central District of the Kruger National Park in August 1965 (Pienaar, 1965) and in August 1979. Distributions are almost identical except for the disappearance of the Western Boundary Sub-population in the southwest (1 dot represents between 1 and 10 wildebeest).

4.3.3 Population structure

Concomitant with the declining and then increasing trends of the wildebeest population, some changes were noted in both the adult sex ratios and also in the cow/calf and cow/yearling ratios. In the case of the adult sex ratio, there was an apparent decline in the proportion of cows to bulls while cow/calf and cow/yearling ratios varied considerably from year to year. Table 4.3.12 presents the data from the four age- and sex classes (adult bulls, adult cows, calves and yearlings) from the three sub-populations and also the combined totals for the whole of the CD as obtained from the quarterly ground counts conducted between January 1978 and January 1984.

4.3.3.1 Adult sex ratio

Table 4.3.13 gives the adult sex ratios from the data in Table 4.3.12 while Figure 4.3.7 illustrates the data. It is immediately apparent that there are two main aspects to the results. Firstly, the initial decline from January 1978 up to January 1981 in the number of cows per bull is clear with little variation in the ratio from count to count while after January 1981 as the proportion of cows decreases (or bulls increases), the sex ratio becomes far more variable.

After January 1981 and in spite of the variability of the data, there was an apparent return to somewhere in the region of the original ratio of 2,5 recorded in 1978.

Table 4.3.12: Sample sizes for the four age and sex classes (adult bulls, adult cows, calves and yearlings) of wildebeest from the three sub-populations as well as the Central District population as a whole as obtained from quarterly ground counts between January 1978 and January 1984.

DATE OF COUNT	POPULATION OR SUB-POPULATION SAMPLED																			
	WESTERN BOUNDARY					SATARA					SWENI/MLONDOZI					WHOLE CD				
	♂♂	♀♀	clv	yrl	n	♂♂	♀♀	clv	yrl	n	♂♂	♀♀	clv	yrl	n	♂♂	♀♀	clv	yrl	n
Jan '78	18	70	32	23	143	36	116	66	35	253	99	219	159	39	516	153	405	257	97	912
Apr	5	22	6	6	39	42	164	73	57	336	85	164	104	54	407	132	350	183	117	782
Jul	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Oct	26	83	38	17	164	72	165	77	28	342	120	251	147	58	576	218	499	262	103	1 082
Jan '79	35	121	86	33	275	38	102	68	32	240	134	246	179	123	682	207	469	333	188	1 197
Apr	34	116	65	30	245	86	175	88	50	399	116	238	163	86	603	236	529	316	166	1 247
July	29	67	32	11	139	49	95	56	27	227	192	318	188	55	753	270	480	276	93	1 119
Oct	34	93	48	16	191	134	226	103	66	529	121	188	105	51	465	289	507	256	133	1 185
Jan '80	21	94	68	42	225	116	108	82	52	358	113	303	243	163	822	250	505	393	257	1 405
Apr	22	131	75	33	261	85	118	81	38	323	176	268	187	103	734	283	517	342	174	1 318
Jul	49	147	96	29	321	161	215	126	56	558	216	267	188	51	722	426	629	410	136	1 601
Oct	31	80	45	16	172	89	154	83	32	358	182	258	162	73	675	302	492	290	121	1 205
Jan '81	28	51	41	20	140	92	125	91	55	363	233	376	312	243	1 164	353	552	444	318	1 667
Apr	34	85	51	37	207	37	202	150	83	472	189	373	275	200	1 037	260	660	476	320	1 716
Jul	56	169	93	32	350	179	273	163	59	674	233	302	203	85	823	468	744	459	176	1 847
Oct	26	88	39	18	171	129	185	124	60	498	72	156	106	39	373	227	429	269	117	1 042
Jan '82	17	60	44	29	150	73	134	99	81	387	129	325	250	202	906	219	519	393	312	1 443
Apr	38	161	94	41	334	146	270	140	80	636	80	210	139	80	509	264	641	373	201	1 479
Jul	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Oct	24	44	27	11	106	218	375	214	136	943	155	266	157	75	653	397	685	398	222	1 702
Jan '83	30	56	40	24	150	188	439	242	211	1 080	191	355	163	222	931	409	850	445	457	2 161
Apr	33	117	65	38	253	156	376	169	87	788	205	397	164	149	915	394	890	398	274	1 956
Jul	21	80	44	25	170	223	420	191	130	964	246	341	101	95	783	490	841	336	250	1 917
Oct	33	100	59	19	211	138	305	144	90	677	160	393	158	165	876	331	798	361	274	1 764
Jan '84	23	52	29	36	140	71	311	200	111	693	79	272	201	60	612	173	635	430	207	1 445

Table 4.3.13: Sex ratios for adult wildebeest in the three sub-populations of the Central District of the Kruger National Park from January 1978 to January 1984

MONTH OF COUNT	Sweni/Mlondozi Sub-population		Satara Sub-population		Western Boundary Sub-population		Whole Central District		Annual average sex ratio	Standard deviation of annual average
	Cows/Bull	n	Cows/Bull	n	Cows/Bull	n	Cows/Bull	n		
January 1978	2,21	318	3,22	152	3,89	88	2,65	558		
April	1,92	249	3,90	206	4,40	27	2,65	482		
July	No count	-	No count	-	No count	-	No count	-		
October	2,09	371	2,29	237	3,19	109	2,29	717	2,53	0,21
January 1979	1,84	380	2,68	140	3,46	156	2,27	676		
April	2,05	354	2,03	261	3,41	150	2,24	765		
July	1,66	510	1,93	144	2,31	96	1,78	750		
October	1,55	309	1,69	360	2,74	127	1,75	796	2,01	0,28
January 1980	2,68	416	0,93	224	4,48	115	2,02	755		
April	1,52	444	1,39	203	5,95	153	1,83	800		
July	1,24	483	1,34	376	3,00	196	1,48	1 055		
October	1,42	440	1,73	243	2,58	111	1,63	794	1,74	0,24
January 1981	1,61	609	1,36	217	1,82	79	1,56	905		
April	1,97	562	5,46	239	2,50	119	2,54	920		
July	1,30	535	1,53	452	3,02	225	1,59	1 212		
October	2,17	228	1,43	314	3,38	114	1,89	656	1,90	0,46
January 1982	2,52	454	1,84	207	3,53	77	2,37	738		
April	2,63	290	1,85	416	4,24	199	2,43	905		
July	No count	-	No count	-	No count	-	No count	-		
October	1,72	421	1,72	593	1,83	68	1,73	1 082	2,18	0,39
January 1983	1,86	546	2,34	627	1,87	86	2,08	1 259		
April	1,94	602	2,41	532	3,55	150	2,26	1 284		
July	1,39	587	1,88	643	3,81	101	1,72	1 331		
October	2,46	553	2,21	443	3,03	133	2,41	1 129	2,12	0,30
January 1984	3,44	351	4,38	382	2,26	75	3,67	808		

Although least squares regression lines were fitted to the data (equations for the two periods were: January 1978 to January 1981: $y = 2,63 - 0,098x$; January 1981 to January 1984: $y = 0,96 + 0,068x$) for the purposes of illustration (Fig. 4.3.7), further least squares regression analyses (r values etc.) are not given as Sokal & Rohlf (1969) deem this a dubious practice on untransformed ratio data. However, using the method for linear regression on r x 2 contingency tables described by Steele & Torrie (1980) on the adult sex ratio data given in Table 4.3.12, the regressions from both these periods were found to be significant. This test was also conducted on the sub-population data for the same two periods, and while the trends for the Western Boundary sub-population were found to be not significant, those from the other two sub-populations were significant. Results of these tests are summarised in Table 4.3.14.

Table 4.3.14: Results from linear regression tests on r x 2 contingency tables on population and sub-population sex ratio data which indicated a decline and subsequent increase in the proportion of cows per bull.

Area	Period			
	Jan. '78 - Jan. 81		Jan. '81 - Jan. '84	
	X^2 value	Probability (df = 1)	X^2 value	Probability (df = 1)
Western Boundary	1,69	$> 0,1$ *	0,18	$> 0,5$ *
Satara	51,99	$< 0,001$	18,45	$< 0,001$
Sweni Mlondozi	16,57	$< 0,001$	9,14	$< 0,005$
Whole Central District	58,22	$< 0,001$	22,39	$< 0,001$

* Not significant

These tests show that in spite of the variability of the data, the trends they show were found to be highly significant in all areas except the Western Boundary sub-population.

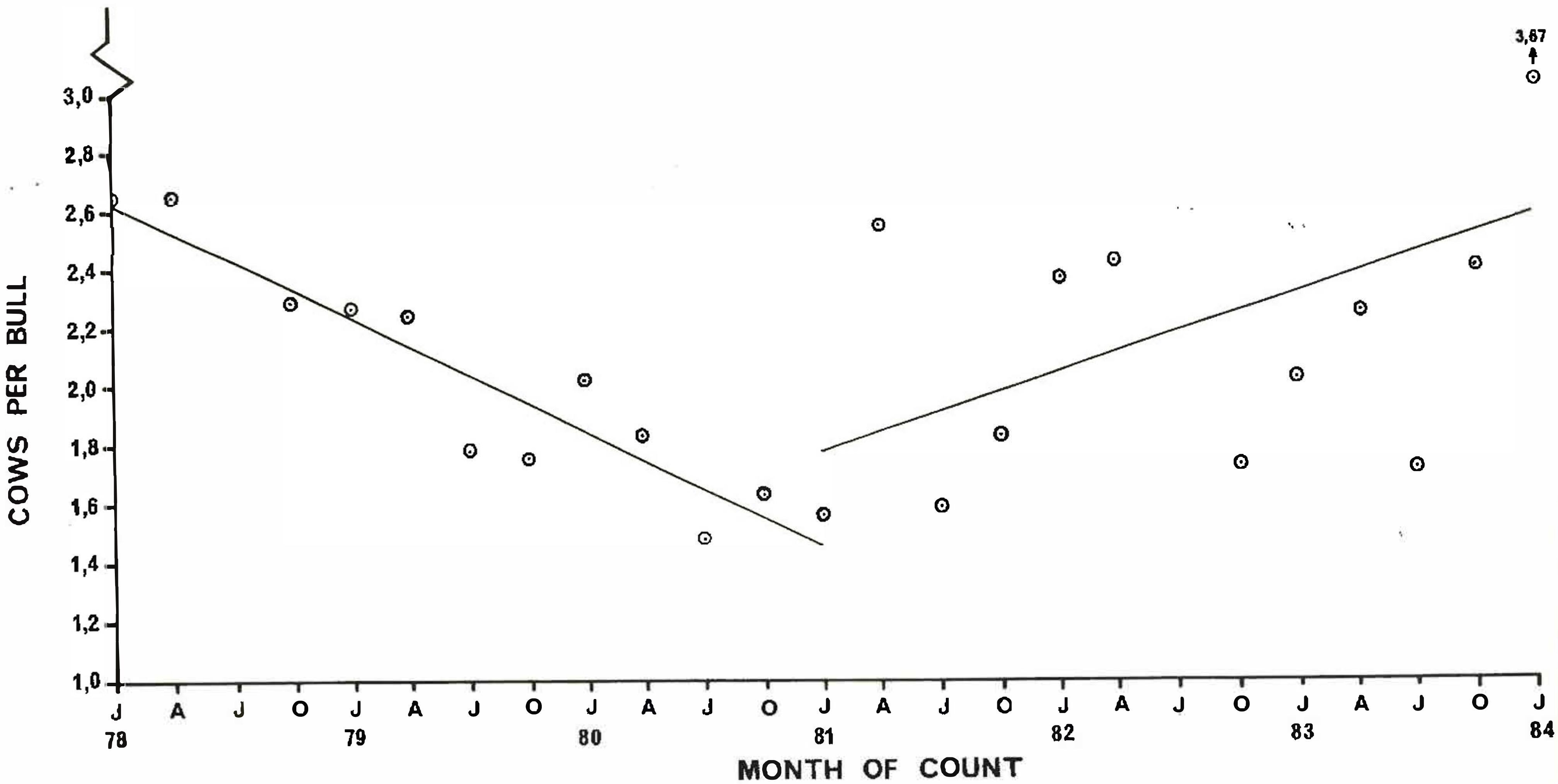


FIGURE 4.3.7: The trend in the sex ratios of adult wildebeest in the Central District of the Kruger National Park. See text for further explanantion.

The variation in the latter counts would appear to be caused by the increasing relative number of bulls in the population who were tending to congregate in larger and larger bachelor herds, and the sex ratio resulting from any one count being greatly influenced by whether these bachelor herds were encountered or not.

The fact that bachelor herds had increased in size and subsequently decreased is well illustrated by Table 4.3.15. This table gives a breakdown of number of bachelor herds from various herd size categories encountered during each count. During the early counts up to January 1980, only one bachelor herd larger than 30 was recorded while from April 1980 onwards, bachelor herds of up to 80 animals and more were encountered. This trend tailed off after January 1981 as after this count no more herds in the >80 or the 51-80 size classes were encountered while after April 1983 none were recorded in even the 31-50 size class.

In order to test whether there had in fact been an increase in the proportion of larger bachelor herds (herds >30), the data from Table 4.3.15 were divided into three periods. These periods were taken as running from October 1978 to January 1980, from April 1980 to July 1981 and from August 1981 to January 1984 consecutively. Chi-squared tests showed that there was a significant increase in herds larger than 30 between the first and second periods (χ^2 = 4,32; df = 1; $P < 0,05$) followed by a decrease again between the second and third periods (χ^2 = 4,76; df = 1; $p < 0,05$). Differences between the first and third periods were not significant (χ^2 = 0,208; df = 1; $p > 0,1$).

Table 4.3.15: Number of wildebeest bachelor herds from various herd size classes encountered during respective ground counts in the Central District of the Kruger National Park between October 1978 and January 1984.

Month of count	Bachelor herd size classes								
	1	2-5	6-10	11-15	16-20	21-30	31-50**	51-80**	80**
	No of herds	No of herds	No of herds	No of herds	No of herds	No of herds	No of herds	No of herds	No of herds
Jan.* 78	-	-	-	-	-	-	-	-	-
Apr.*	-	-	-	-	-	-	-	-	-
Oct.	73	25	5	2	1	0	0	0	0
Jan. 79	57	31	6	1	1	0	0	0	0
Apr.	86	51	5	1	0	0	0	0	0
Jul.	36	21	1	2	3	0	0	0	1(90)
Oct.	76	24	4	3	3	0	0	0	0
Jan. 80	93	29	3	1	2	0	0	0	0
Apr.	110	17	3	0	2	0	0	1(65)	0
Jul.	99	26	8	3	3	0	1(45)	1(52)	0
Oct.	113	33	3	1	2	0	0	1(54)	0
Jan. 81	88	12	0	2	0	0	0	1(59)	1(124)
Apr.	140	18	1	0	1	2	0	0	0
Jul.	137	34	17	2	0	2	1(33)	0	0
Oct.	103	27	4	1	0	0	0	0	0
Jan. 82	130	12	2	2	1	0	0	0	0
Apr.	150	15	5	1	1	0	0	0	0
Oct.	84	26	8	4	3	1	1(33)	0	0
Jan. 83	130	49	11	1	1	0	0	0	0
Apr.	216	31	4	0	2	0	1(31)	0	0
Jul.	159	37	11	4	1	2	0	0	0
Oct.	146	41	4	2	0	0	0	0	0
Jan. 84	99	12	3	0	0	1	0	0	0

* No breakdown of raw data available.
** Numbers in brackets indicate actual herd sizes. (Herds>31).

These large bachelor herds presented a problem in the analysis of the data. Some of these herds were so large (up to 124) that their inclusion in the analysis greatly skewed the sex ratio of the samples. However, they were obviously an important component of the population at that time and as such they could not be excluded from the analysis.

The extreme variability of these sex ratio data make interpretation difficult but when the four ratios from each respective year are averaged, the variability is largely eliminated and the trends in the sex ratio become more evident.

Table 4.3.16 gives the annual average of the adult sex ratios from each sub-population and also from the total population while Figure 4.3.8 graphically shows the trend. Significance tests were not conducted on the data in this table as the trends have already been shown to be significant in Table 4.3.14.

Table 4.3.16 Annual averages in the sex ratio (cows per bull) of adult wildebeest from quarterly ground counts in the Central District of the Kruger National Park between 1978 and 1984.

Year of count	n*	Sweni/Mlondozi Sub-population		Satara Sub-population		Western Boundary Sub-population		Whole Central District	
		Ratio	S.D.**	Ratio	S.D.**	Ratio	S.D.**	Ratio	S.D.**
1978	3	2,07	0,15	3,14	0,81	3,83	0,61	2,53	0,21
1979	4	1,76	0,22	2,08	0,42	2,98	0,55	2,01	0,28
1980	4	1,72	0,65	1,33	0,33	4,00	1,53	1,74	0,24
1981	4	1,76	0,39	1,44***	0,09	2,68	0,68	1,90	0,46
1982	3	2,29	0,50	1,80	0,07	3,20	1,24	2,18	0,39
1983	4	1,91	2,21	2,21	0,24	3,07	0,86	2,12	0,30
1984	1	3,44	-	4,38	-	2,26	-	3,67	-

* n = Number of counts
** S.D. = Standard Deviation
*** The ratio for this area in April 1981 was 5,46 (see Table 4.3.13) which is obviously anomalous due to sampling variation and has therefore been exluded from this calculation. The average and S.D. were calculated on the data from the other three counts from 1981.

Thus it is clear that there had indeed been a decline in the proportion of cows to bulls in the population from 1978 to 1980 followed by an increase. As only one count was conducted during 1984 (January) and this produced a very high proportion of cows (3,67 cows per bull), little interpretive value can be attached to it. At best it can be said that there was a probable further increase in the proportion of adult cows.

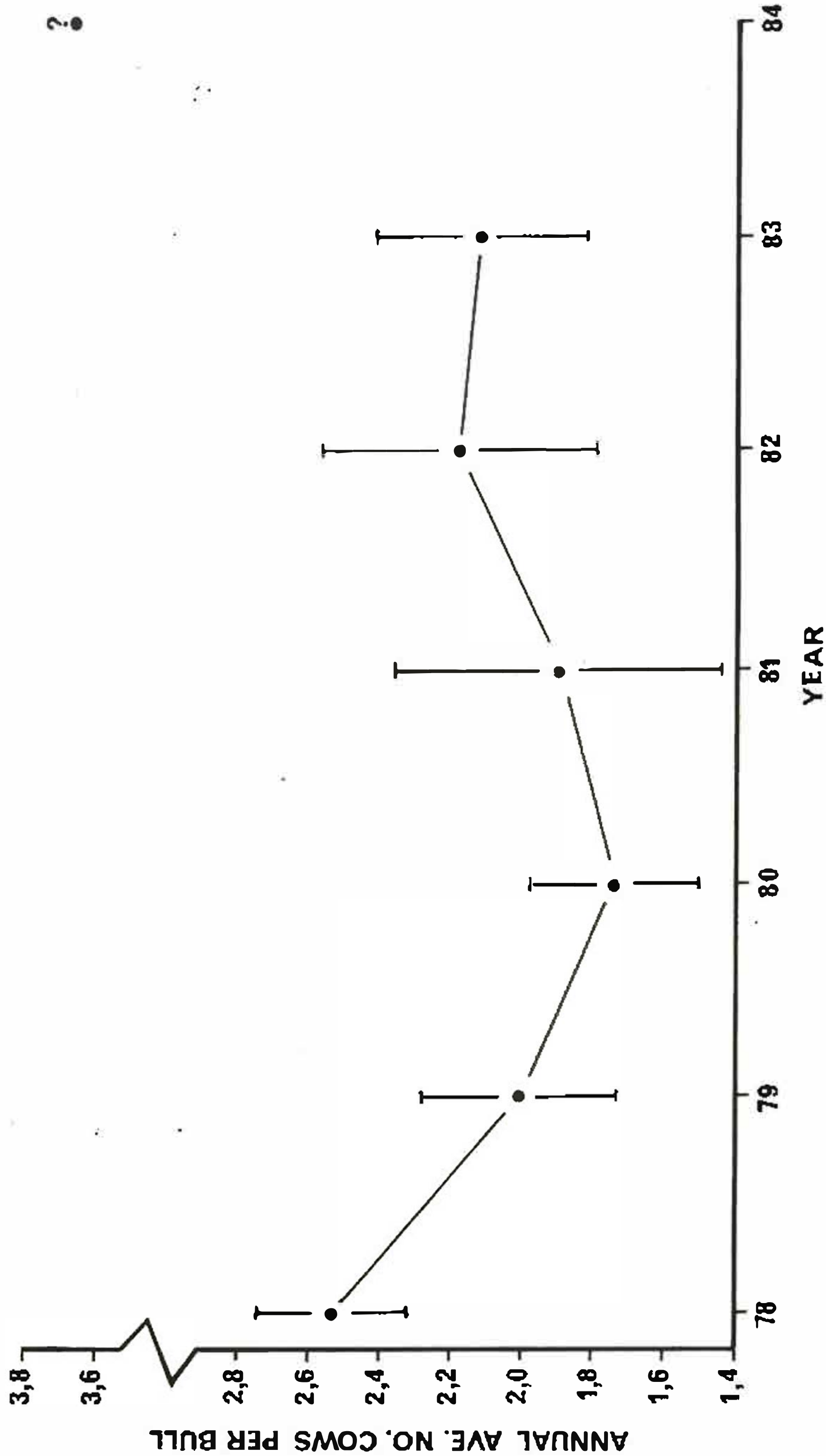


FIGURE 4.3.8: The trends in the adult sex ratio of wildebeest in the Central District of the Kruger National Park from the annual average of respective quarterly ground counts. Vertical lines indicate one standard deviation.

Averages for the three sub-populations were plotted graphically (Figure 4.3.9) and this shows that the distortion in the sex-ratio occurred in both the Satara and Sweni/Mlondozi sub-populations though it was far more pronounced in the Satara sub-population.

Further evidence for this decline comes from the trend in the percentage of adult cows in the population from respective counts. In Table 4.3.17 the percentages of both adult bulls and adult cows are given from each respective count.

Table 4.3.17: The percentages of adult wildebeest bulls and cows in the population of the Central District of the Kruger National Park, obtained from quarterly ground counts.

Date of count	% Bulls	% Cows
Jan. 78	16,8	44,4
Apr.	16,9	44,8
Oct.	20,1	46,1
Jan. 79	17,3	39,2
Apr.	18,9	42,4
Jul.	24,1	42,9
Oct.	24,4	42,9
Jan. 80	17,8	35,9
Apr.	21,5	39,2
Jul.	26,6	39,3
Oct.	25,1	40,8
Jan. 81	21,2	33,1
Apr.	15,2	38,5
Jul.	25,3	40,3
Oct.	21,8	41,2
Jan. 82	15,2	36,0
Apr.	17,8	43,3
Oct.	23,3	40,2
Jan. 83	18,9	39,3
Apr.	20,1	45,5
Jul.	25,6	43,9
Oct.	18,8	45,2
Jan. 84	12,0	43,9

No clear trends are discernible in the data presented in this table. The variability in the bachelor group sizes is once again largely responsible for the variation recorded in the percentage of bulls. However, when the percentages of cows in the population are plotted graphically, two clear trends emerge.

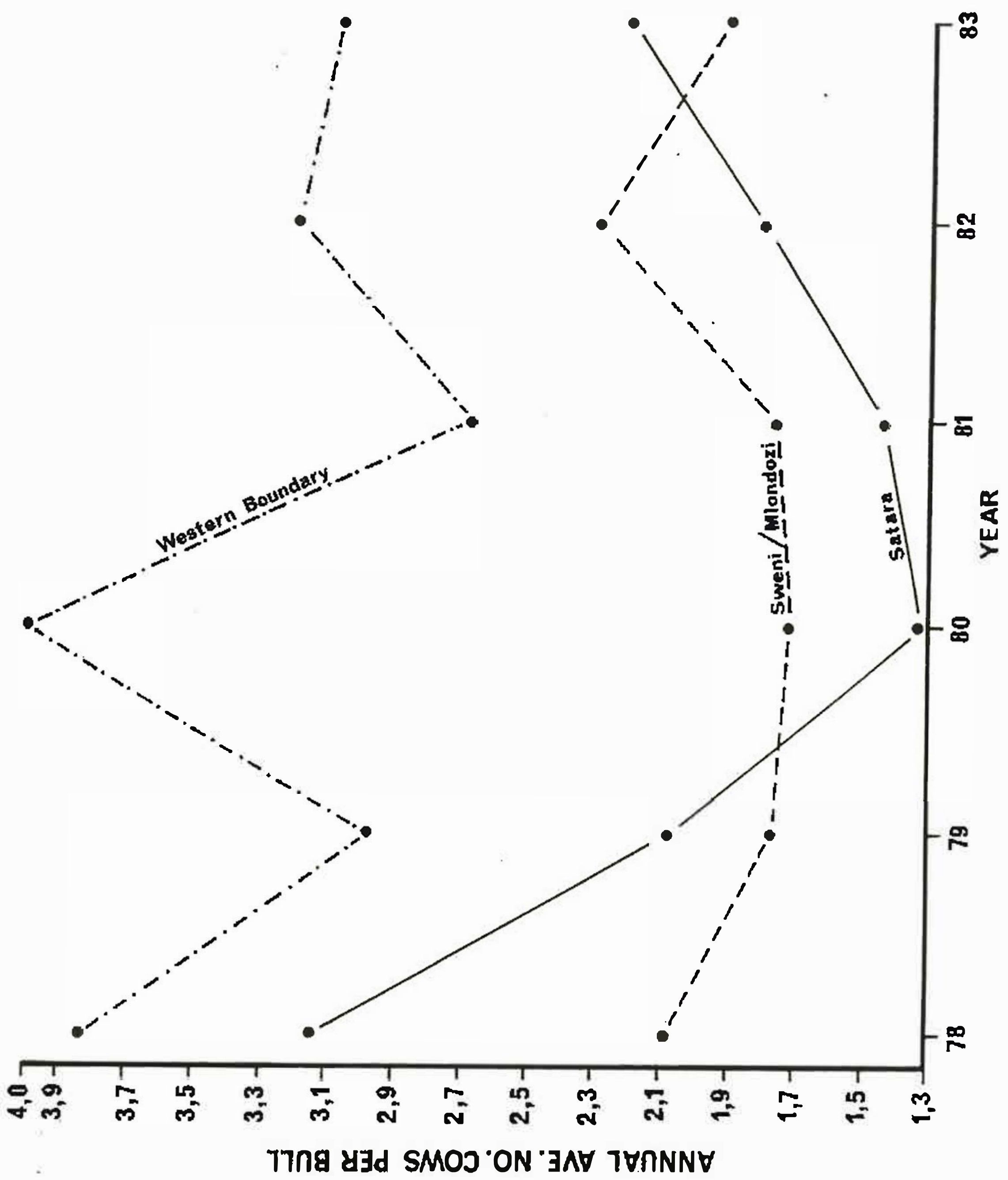


FIGURE 4.3.9: Trends in the average annual sex ratios of the three wildebeest sub-populations of the Central District of the Kruger National Park between 1978 and 1983.

The first is an annual trend - the percentage of adult cows is always at its lowest in January which is just after the calving peak. This is because at this time there is a high proportion of new-born calves in the population which results in a lowered percentage of adult cows. As calf mortality is higher than adult mortality during the year, the proportion of adult cows in the population increases. This can be clearly seen year after year in Figure 4.3.10 (dotted lines showing the annual trends were fitted by eye for the purposes of illustration only).

To test the significance of this annual trend a chi-squared test was conducted on pooled totals from January counts against those from October counts. A total of 3 935 and 3 410 adult cows were counted during January and October counts respectively while the rest of the samples were made up of 6 295 and 4 570 other individuals for the respective two months. A significantly smaller proportion of cows was counted in January than in October counts (χ^2 = 33,73; $p < 0,001$).

The second trend is once again the decline in the proportion of adult cows in the population from January 1978 to January 1981 after which there was a return to a more normal percentage.

As there is considerable variation in the proportions during any one year due to calf mortality, only counts conducted at the same time of year are comparable (i.e. when population structure, especially the percentage of calves should be much the same). Bearing in mind the limitations of using the method of least squares regression on untransformed data (Sokal & Rohlf, 1969), straight lines have been fitted to January counts (arrowed) for both the decline and incline phases for the purpose of illustration. As these trends have already been shown to be significant, no further statistical analyses were conducted.

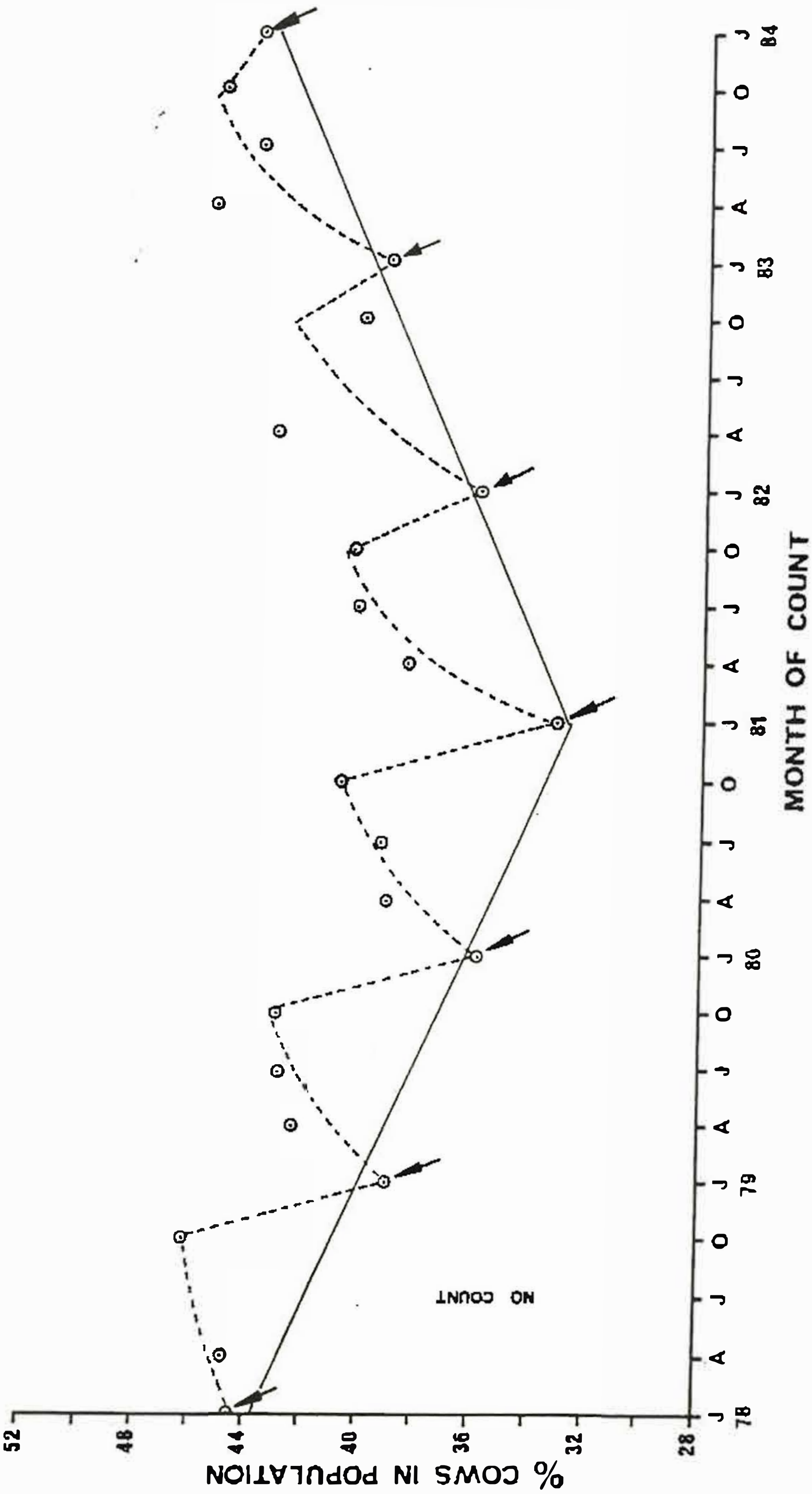


FIGURE 4.3.10: Trends in the percentage of adult cows in the wildebeest population of the Central District of the Kruger National Park. The decline in and subsequent increase in the proportion is evident as is the yearly trend - lowered proportion of cows while there is a large proportion of newborn calves (see text for further explanation)

After examining the adult sex ratio from all these various perspectives, there remains little doubt that a distortion took place in favour of the bulls but the question that arises is: What caused the skewing?

Table 4.3.17 gave the percentages of bulls and cows recorded during each ground count. Using these percentages, and having reasonably accurate population estimates from aerial survey data (Joubert, 1978, 1979, 1980, 1981, 1982, 1983c, 1984), it was possible to esimate the actual number of bulls and cows in the population. As the percentages were variable from count to count, those from each year were averaged to minimise variability. Table 4.3.18 gives population estimates, average percentages of bulls and cows and the estimates of numbers of both.

These estimates suggest that while there was an initial decline in the number of cows from 1978 to 1980 followed by a steep increase, bulls were increasing in number during the whole period. Thus from 1978 to 1980, cows were dying while bulls were surviving resulting in the skewed sex ratio. Figure 4.3.11 presents the data graphically but includes the population trends (from aerial survey data). This shows that while the population was declining between 1978 and 1979, the number of cows was also decreasing but between 1979 and 1980 when the population had started to increase the number of cows still decreased marginally and only subsequent to 1980 did they start to increase again. This they did at an increasing rate. The observed rate of increase ($\bar{r}$) for this segment of the population over this period was calculated as 0,785 (see page 116 for other calculations of $\bar{r}$). Bulls on the other hand, increased at a rate of $\bar{r}$ = 0,376.

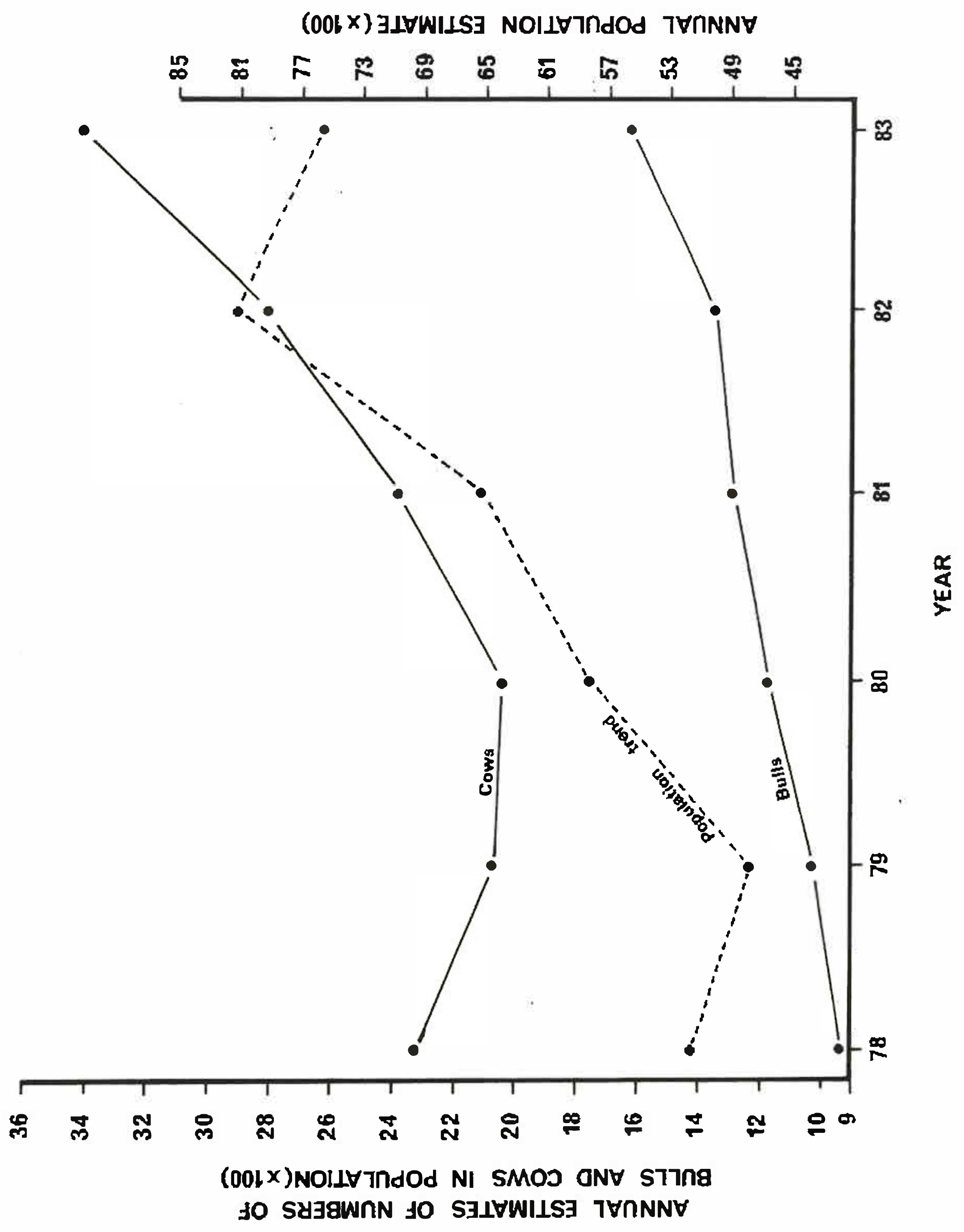


FIGURE 4.3.11: The trends in the number of wildebeest bulls and cows in the population of the Central District of the Kruger National Park between 1978 and 1983.

Table 4.3.18: Quarterly estimates of actual numbers of wildebeest bulls and cows in the Central District of the Kruger National Park between 1978 and 1983 as well as annual averages.

Year and month of count	Population Estimate	% Bulls	Estimated no. of bulls	Yearly average	% Cows	Estimated no. of cows	Yearly average
Jan. 78	5 141	16,8	864		44,4	2 283	
Apr.	"	16,9	869		44,8	2 303	
Oct.	"	20,1	1 033	929	46,1	2 370	2 319
Jan. 79	"	17,3	889		39,2	2 015	
Apr.	"	18,9	972		42,4	2 180	
Jul.	4 768	24,1	1 149		42,9	2 045	
Oct.	"	24,4	1 163	1 043	42,9	2 045	2 071
Jan. 80	"	17,8	849		35,9	1 712	
Apr.	"	17,7	844		39,3	1 874	
Jul.	5 816	26,6	1 547		39,3	2 286	
Oct.	"	25,1	1 460	1 175	40,8	2 373	2 045
Jan. 81	"	21,2	1 233		33,1	1 925	
Apr.	"	15,2	884		38,5	2 293	
Jul.	6 512	25,3	1 648		40,3	2 624	
Oct.	"	21,8	1 420	1 296	41,2	2 683	2 381
Jan. 82	"	15,2	990		36,0	2 344	
Apr.	"	17,8	1 159		43,3	2 819	
Oct.	8 127	23,3	1 894	1 348	40,3	3 275	2 812
Jan. 83	"	18,9	1 536		39,3	3 194	
Apr.	"	20,1	1 634		45,5	3 698	
Jul.	7 584	25,6	1 942		43,9	3 329	
Oct.	"	18,8	1 426	1 634	45,2	3 427	3 412

The data presented here imply that while there was an increase in the population between 1979 and 1980, there was actually a slight decrease in the number of cows. For this to have been possible there must have been a high recruitment rate, which in this case means a high survival rate of the previous year's calves as well as high birth and survival rates of that year's calves, while between 1982 and 1983, there was a decrease in the total population but the numbers of both adult bulls and cows actually increased. This suggests a very high mortality in the other segments of the population - the calves and yearlings.

4.3.3.2 Cow/calf and cow/yearling ratios

The determination of the survival rates of calves and yearlings was the main focus of the quarterly population structure counts. Survival rates are extremely difficult to measure. As it is impossible to get actual counts of the absolute numbers of calves in the population at various intervals during the year and so to measure actual mortality, the decrease in the number of calves has to be inferred from the proportions of various age classes in the population.

It is clearly impossible to count all calves in a population and so the proportions of each age class have to be estimated from ground counts, and changes in these propotions may then reflect changes in the structure which would indicate differential survival/mortality rates among the various age and/or sex classes.

It would be possible to gain some idea of calf mortality rates from the varying percentages of calves in the population but as the proportion of bulls recorded during counts is unreliably variable, and their inclusion in the calculation of calf percentages would cloud this aspect as well. Furthermore, the proportion of yearlings declines due to mortality as time goes on which would also affect the percentage of calves in the population. Cows and calves however, are always together and thus there is an equal probability of encountering each of these classes during random ground counts.

In this study therefore calf mortality was measured as the proportion of calves to adult cows. As wildebeest are such highly seasonal breeders (Braack 1973; Watson, 1969) it is an easy matter to achieve some reasonably accurate measure of the mortality rates from the declining proportion of calves to cows because after the calving season, there are no (or very few) subsequent births later in the year which would veil the actual mortality rate. However, the mortality rate of adult cows remains uncertain. Although population totals are estimated reasonably accurately from aerial surveys, this is only done once per year. It is thus possible to get a reasonable estimate of the actual number of cows in the population only once per year from the percentage of cows (obtained from ground counts) in the population at the time of the aerial surveys. Aerial surveys of the CD are conducted in July as were one of the quarterly ground counts, but obviously, censuses conducted only once per year are unsuitable for the estimation of mortality throughout the year. Thus these measures of calf and yearling mortality take no account of mortality rates of adult cows and they are not measures of absolute mortality. However, they do provide a useful means of comparing mortality rates between populations spatially and temporarily. Tables 4.3.19 to 4.3.22 present the cow:calf ratios obtained during ground counts.

To estimate the required sample sizes for two levels of precision (± 5,0 and ± 7,5 calves per 100 cows respectively) and to determine the confidence intervals for the actual sample sizes obtained, the statistical procedures given in Anonymous (1977) were applied to these cow/calf and cow/yearling data from the whole CD population (see Table 4.3.23).

Table 4.3.19: Wildebeest cow/calf ratios from the Western Boundary sub-population rates showing survival of respective calf cohorts during the first two years of life obtained from quarterly ground counts between 1978 and 1984

Time of count	Parameter	Western Boundary Sub-population							
		Calves born in January of:							
		1977	1978	1979	1980	1981	1982	1983	1984
January (Month of birth)	Cows:calves Calves/100 cows % calves in pop.	- - -	70:32 45,7 22,4	121:86 71,1 31,3	94:68 72,3 30,2	51:41 80,4 29,3	60:44 73,3 29,3	56:40 71,4 26,7	52:29 55,8 20,7
April	Cows:calves Calves/100 cows % calves in pop.	- - -	22:6 27,3 16,7	116:65 56,0 26,5	131:75 57,3 28,7	85:51 60,0 24,6	161:94 58,4 28,1	117:65 55,6 25,7	- - -
July	Cows:calves Calves/100 cows % calves in pop.	- - -	No count	67:32 47,8 23,0	147:96 65,3 29,9	169:93 55,0 26,5	No count	80:44 55,0 25,9	- - -
October	Cows:calves Calves/100 cows % calves in pop.	- - -	83:38 45,8 23,1	93:48 51,6 25,1	80:45 56,3 26,2	88:39 44,3 22,8	44:27 61,4 25,5	100:59 59,0 27,96	- - -
January	Cows: yearlings Yearl./100 cows % yearl. in pop.	70:23 32,8 16,1	121:33 27,3 12,0	94:42 44,7 18,6	51:20 39,2 14,3	60:29 43,3 19,3	56:24 42,9 16,0	52:36 69,2 25,7	- - -
April	Cows:yearlings Yearl./100 cows % yearl. in pop.	22:6 27,3 16,7	116:30 25,9 12,2	131:33 25,2 12,6	85:37 43,5 17,9	161:41 25,5 12,3	117:38 32,5 15,0	- - -	- - -
July	Cows:yearlings Yearl./100 cows % yearl. in pop.	No count	67:11 16,4 7,9	147:29 19,7 9,0	169:32 18,9 9,1	No count	80:25 31,3 14,7	- - -	- - -
October	Cows:yearlings Yearl./100 cows % yearl. in pop.	83:17 20,3 10,4	93:16 17,2 8,3	80:16 22,5 9,3	88:18 20,5 10,5	44:11 25,0 10,4	100:19 19,0 9,0	- - -	- - -

Table 4.3.20: Wildebeest cow/calf ratios from the Satara sub-population showing survival rates of respective calf cohorts during the first two years of life obtained from quarterly ground counts between 1978 and 1984

Time of count	Parameter	Satara Sub-population							
		Calves born in January of:							
		1977	1978	1979	1980	1981	1982	1983	1984
January (Month of birth)	Cows:calves Calves/100 cows % calves in pop.	- - -	116:66 56,9 26,1	102:68 66,7 28,3	108:82 75,9 22,9	125:91 72,8 25,1	134:99 73,9 25,6	439:242 55,1 22,4	311:200 64,3 28,9
April	Cows:calves Calves/100 cows % calves in pop.	- - -	164:73 44,5 21,7	175:88 50,3 22,1	118:81 68,6 25,1	202:150 74,3 31,8	270:140 51,9 22,0	376:169 44,95 21,5	- - -
July	Cows:calves Calves/100 cows % calves in pop.	- - -	No count	95:56 58,9 24,7	215:126 58,6 22,6	273:163 59,7 24,2	No count	420:191 45,5 19,8	- - -
October	Cows:calves Calves/100 cows % calves in pop.	- - -	165:77 46,7 22,5	226:103 45,6 19,5	154:83 53,9 23,2	185:124 67,0 24,9	375:214 57,1 22,7	305:144 47,2 21,3	- - -
January	Cows: yearlings Yearl./100 cows % yearl. in pop.	116:35 30,2 13,8	102:32 31,4 13,3	108:52 41,1 14,5	125:55 44,0 15,2	134:81 60,5 20,9	439:211 48,1 19,5	311:111 35,7 16,0	- - -
April	Cows:yearlings Yearl./100 cows % yearl. in pop.	164:57 34,8 17,0	175:50 28,6 12,5	118:38 32,2 11,8	202:83 41,1 17,6	270:80 29,6 12,6	376:87 23,1 11,0	- - -	- - -
July	Cows:yearlings Yearl./100 cows % yearl. in pop.	No count	95:27 28,4 11,9	215:56 26,0 10,0	273:59 21,6 8,8	No count	420:130 30,95 13,5	- - -	- - -
October	Cows:yearlings Yearl./100 cows % yearl. in pop.	165:28 17,0 8,2	226:66 29,2 12,4	154:32 20,8 8,9	185:60 32,4 12,1	375:136 36,3 14,4	305:90 29,5 13,3	- - -	- - -

Table 4.3.21: Wildebeest cow/calf ratios from the Sweni/Mlondozi sub-population showing survival rates of respective calf cohorts during the first two years of life obtained from quarterly ground counts between 1978 and 1984

Time of count	Parameter	Sweni/Mlondozi Sub-population							
		Calves born in January of:							
		1977	1978	1979	1980	1981	1982	1983	1984
January (Month of birth)	Cows:calves Calves/100 cows % calves in pop.	- - -	219:159 72,6 38,8	246:179 72,8 26,2	303:243 80,2 29,6	376:312 83,0 26,7	325:250 76,9 27,6	355:163 45,9 17,5	272:201 73,9 32,8
April	Cows:calves Calves/100 cows % calves in pop.	- - -	164:104 63,4 25,6	238:163 68,5 27,0	268:187 69,8 25,5	373:275 73,7 26,5	210:139 66,2 27,3	397:164 41,3 17,9	- - -
July	Cows:calves Calves/100 cows % calves in pop.	- - -	No count	318:188 59,1 25,0	267:188 70,4 26,0	302:203 67,2 24,7	No count	341:101 29,6 12,9	- - -
October	Cows:calves Yearl./100 cows % yearl. in pop.	- - -	251:147 58,6 25,5	188:105 55,9 22,6	258:162 62,8 24,0	156:106 67,95 28,4	266:157 59,0 24,0	393:158 40,2 18,0	- - -
January	Cows:yearlings Calves/100 cows % calves in pop.	219:39 17,8 7,6	246:123 50,0 18,0	303:163 53,8 19,8	376:243 64,6 20,8	325:202 62,2 22,3	355:222 62,5 23,9	272:60 22,1 9,8	- - -
April	Cows: yearlings Yearl./100 cows % yearl. in pop.	164:54 32,9 13,3	238:86 36,1 14,3	268:103 38,4 14,0	373:200 53,6 19,3	210:80 38,1 15,7	397:149 37,5 16,3	- - -	- - -
July	Cows:yearlings Yearl./100 cows % yearl. in pop.	No count	318:55 17,3 7,3	267:51 19,1 7,1	302:85 28,2 10,3	No count	341:95 27,9 12,1	- - -	- - -
October	Cows:yearlings Yearl./100 cows % yearl. in pop.	251:58 23,1 10,0	188:51 27,1 10,9	258:73 28,3 10,8	156:39 25,0 10,5	266:75 28,2 11,5	393:165 41,98 18,8	- - -	- - -

Table 4.3.22: Wildebeest cow/calf ratios from the whole Central District population showing survival rates of respective calf cohorts during the first two years of life obtained from quarterly ground counts between 1978 and 1984

Time of count	Parameter	Whole Central District Population							
		Calves born in January of:							
		1977	1978	1979	1980	1981	1982	1983	1984
January (Month of birth)	Cows:calves Calves/100 cows % calves in pop.	- - -	405:257 63,5 28,2	469:333 71,0 27,8	505:393 77,8 28,0	552:444 80,4 26,6	519:393 75,2 27,2	850:445 52,4 20,6	635:430 67,7 29,8
April	Cows:calves Calves/100 cows % calves in pop.	- - -	350:183 52,3 23,4	529:316 59,7 25,3	517:342 66,2 25,9	660:476 72,1 27,7	641:373 58,2 25,2	890:398 44,7 20,4	- - -
July	Cows:calves Calves/100 cows % calves in pop.	- - -	No count	480:276 57,5 24,7	629:410 65,2 25,6	744:459 61,7 24,9	No count	841:336 39,95 17,5	- - -
October	Cows:calves Calves/100 cows % calves in pop.	- - -	499:262 52,5 24,2	507:256 50,5 21,6	492:290 58,9 24,1	429:269 62,7 25,8	685:398 58,1 23,4	798:361 45,2 20,5	- - -
January	Cows: yearlings Yearl./100 cows % yearl. in pop.	405:97 24,0 10,6	469:188 40,1 15,7	505:257 50,9 18,3	552:318 57,6 19,1	519:312 60,1 21,6	850:457 53,8 21,2	635:207 32,6 14,3	- - -
April	Cows:yearlings Yearl./100 cows % yearl. in pop.	350:117 33,4 15,0	529:166 31,4 13,3	517:174 33,7 13,2	660:320 48,5 18,7	641:201 31,4 13,6	890:274 30,8 14,0	- - -	- - -
July	Cows:yearlings Yearl./100 cows % yearl. in pop.	No count	480:93 19,4 8,3	629:136 21,6 8,5	744:176 23,7 9,5	No count	841:250 29,7 13,0	- - -	- - -
October	Cows:yearlings Yearl./100 cows % yearl. in pop.	499:103 20,6 9,5	507:133 26,2 11,2	492:121 24,6 10,0	429:117 27,3 11,2	685:222 32,4 13,0	798:274 34,3 15,5	- - -	- - -

Table 4.3.23: Statistical estimates of desired sample size for the acquisition of reliable cow/calf ratio data of wildebeest in the Central District of the Kruger National Park and estimates of confidence intervals for respective counts based on actual sample sizes*

Date	Pop. size	% Cows + calves in population	Est. No. of cows + calves in population	Cow/ calf ratio	Desired Precision		Student's "t" value	n		Cows + calves actually counted	Confidence interval
					A	B		A	B		
Jan. 78	5 141	73	3 753	63	5,0	7,5	1,645	1 222	663	662	± 7,5
Apr.	"	68	3 496	52	"	"	"	947	496	533	" 7,2
Jul.	-	-	-	-	-	-	-	-	-	-	-
Oct.	5 141	70	3 599	52	5,0	7,5	1,645	955	498	761	± 5,8
Jan. 79	"	67	3 444	71	"	"	"	1 359	774	802	" 7,3
Apr.	"	68	3 496	60	"	"	"	1 126	610	845	" 6,1
Jul.	4 768	68	3 242	58	"	"	"	1 056	573	756	" 6,3
Oct.	"	64	3 052	51	"	"	"	891	472	763	" 5,6
Jan. 80	"	64	3 052	78	"	"	"	1 426	856	898	" 7,2
Apr.	"	65	3 099	66	"	"	"	1 204	682	859	" 6,4
Jul.	5 816	65	3 780	65	"	"	"	1 271	695	1 039	" 5,8
Oct.	"	65	3 780	59	"	"	"	1 131	603	782	" 6,4
Jan. 81	"	60	3 490	80	"	"	"	1 555	919	996	" 7,1
Apr.	"	66	3 839	72	"	"	"	1 440	809	1 136	" 6,0
Jul.	6 512	65	4 233	62	"	"	"	1 244	661	1 203	" 5,1
Oct.	"	67	4 363	63	"	"	"	1 280	680	698	" 7,4
Jan. 82	"	63	4 103	76	"	"	"	1 571	888	912	" 7,4
Apr.	"	69	4 493	58	"	"	"	1 162	603	1 014	" 5,4
Jul.	8 127	-	-	-	-	-	-	-	-	-	-
Oct.	"	64	5 201	58	5,0	7,5	1,645	1 204	614	1 083	± 5,4
Jan. 83	"	60	4 876	52	"	"	"	1 027	517	1 295	" 4,3
Apr.	"	66	5 364	45	"	"	"	859	420	1 288	" 3,9
Jul.	7 584	61	4 626	40	"	"	"	717	349	1 177	" 3,7
Oct.	"	66	5 005	45	"	"	"	850	417	1 159	" 4,1
Jan. 84	"	74	5 612	68	"	"	"	1 561	793	1 065	" 6,3

* See key to Table 4.3.25 overleaf.

Key to Table 4.3.23

Column 1 Date: Month of count

Column 2 Population size: From most recent aerial survey data.

Column 3 % cows plus calves in population: Percentages calculated from actual data from respective ground counts.

Column 4 Estimated total number of cows plus calves in population: The percentage of cows plus calves in Column 3 of the total population size from Column 2.

Column 5 Sex ratio: Ratios calculated from actual data from respective ground counts given as calves per 100 cows.

Column 6 Desired precision: The desired precision of the count. Two levels of precision are presented: $\pm$ 5(A) and $\pm$ 7,5(B) calves per 100 cows.

Column 7 Student's "t" value: The value of the two-tailed student's "t" with infinite degrees of freedom at an alpha level of 0,1.

Column 8 n: The desired sample sizes calculated for the two levels of precision (A) and (B) in Column 6. (See "Methods").

Column 9 The total number of cows plus calves actually counted during each respective count (compare these totals with those in Column 7).

Column 10 Confidence interval: The confidence interval for each count based on data obtained during that particular count (e.g. for January 1978 the ratio was calculated at 63 ($\pm$ 7,5) calves per 100 cows.

The cow/calf ratio data are much more consistent than was the case with the adult sex ratio data (Table 4.3.23). Differences in ratios from count to count are more a reflection of actual calf mortality than of sample variation. These statistical procedures are therefore more reliable on cow/calf ratio data than on adult sex ratio data because each breeding herd contains both cows and calves and is thus a reflection of the actual ratio while in the case of adult sex ratios bull groups are highly variable in size and are usually discrete from breeding herds. Each bull group therefore influences the sex ratio sample rather than contributing towards it.

The confidence intervals for these cow/calf ratios varied between $\pm$ 3,7 and $\pm$ 7,5 with a mean of $\pm$ 5,99 and a standard deviation of 1,18.

Figure 4.3.12 is a graphic presentation of the cow/calf ratios given in Table 4.3.22 and illustrates the large variation in survival rates of calves from various cohorts. Counts were started in 1978 and thus the calves born in January 1977 were already one year old at that time and there are consequently no data for them on their first year of life. Counts were terminated in January 1984 and there is therefore only one data point for calves born in January 1984 while calves born in January 1983 were only a year old when counts were terminated. There is therfore no information on their second year of life.

For the purposes of illustration, least squares regression lines have been fitted to the data points of each respective calf cohort and Table 4.3.24 gives their equations, though once again, due to the untransformed nature of the data, no further least squares regression analyses were conducted. However, the method of Steele and Torrie (1980) for linear regression on r x 2 contingency tables is applicable to these data as was the case with the adult sex ratio data. Table 4.3.26 also gives the results of these analyses on respective cohorts.

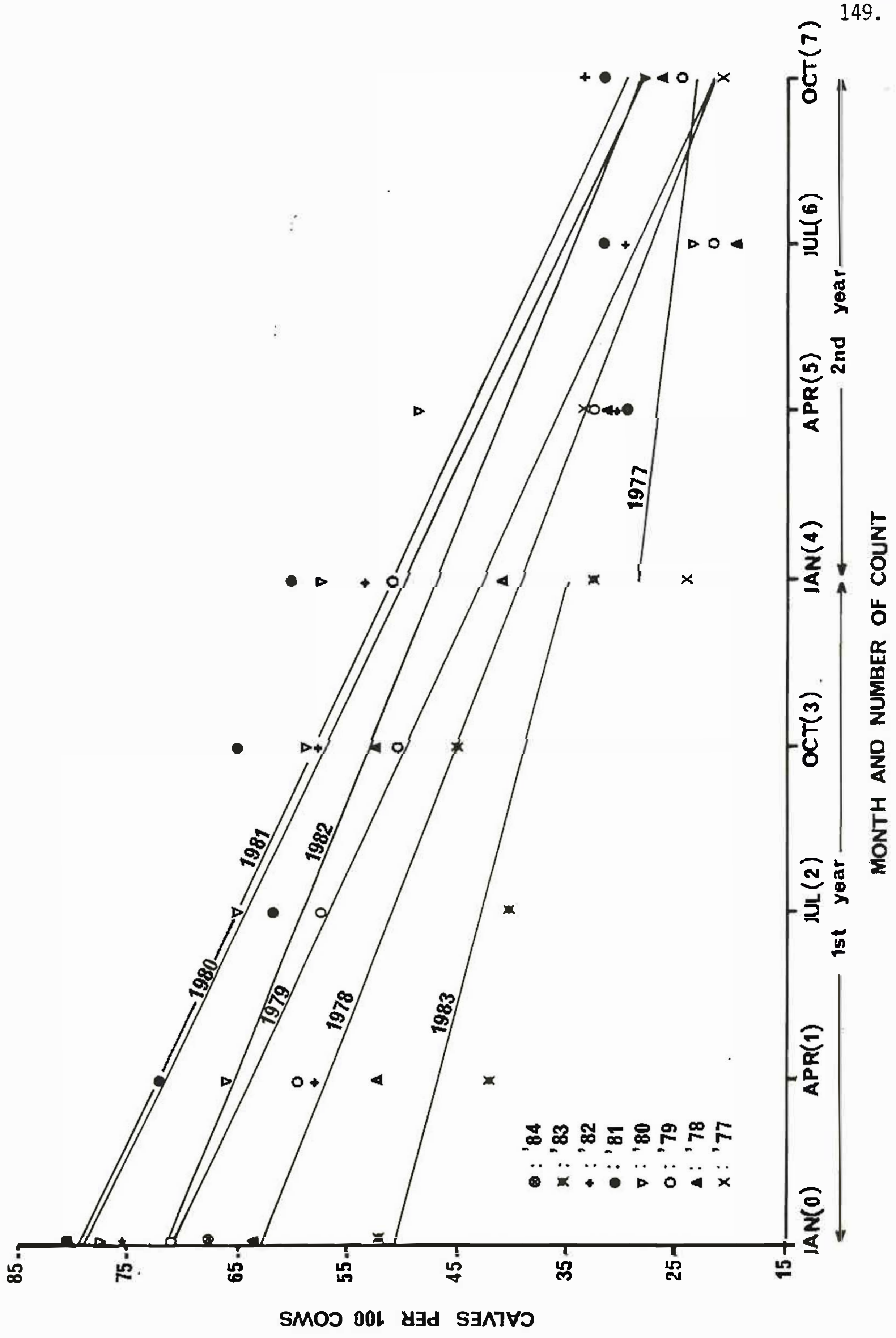


FIGURE 4.3.12: Wildebeest cow/calf ratios from respective calf cohorts between 1977 and 1984 from the Central District of the Kruger National Park with least squares regression lines fitted to show survival during the first 21 months of life. See text for further explanation.

Table 4.3.24: Equations,("a" and "b" values) of least-squares linear regression lines and χ^2 values, degrees of freedom and probabilities from linear regression analyses on r x 2 contingency tables from respective calf cohorts from the wildebeest population of the Central District of the Kruger National Park between January 1978 and January 1984 (see Figure 4.3.12).

Year of birth	No. of counts	Least squares regression analysis		Linear regression on r x 2 contingency tables		
		a *	b **	χ^2 +	df ++	p +++
1977	3	36,1	- 1,89	2,55	1	$>0,1$
1978	7	62,7	- 5,91	108,12	1	$<0,001$
1979	8	70,4	- 6,85	164,99	1	$<0,001$
1980	8	78,9	- 7,35	164,61	1	$<0,001$
1981	7	79,9	- 7,22	136,63	1	$<0,001$
1982	7	71,5	- 6,17	143,09	1	$<0,001$
1983	5	50,8	- 3,91	17,36	1	$<0,001$
1984	1	-	-	-	-	-

* a = "a" value from the straight line equation $y = a + bx$
** b = "b" value from the straight line equation $y = a + bx$
\+ χ^2 = Chi-squared value
++ df = Degrees of freedom
+++ p = probability that such a correlation exists.

Using the Wilcoxon matched-pairs signed-ranks test, it could also be shown that differences may exist between the data sets of some cohorts (e.g. between 1979 and 1980, the only cohorts to have been sampled during every quarter of their first two years of life, a significant difference was detected (Wilcoxon's T = 0; $p<0,01$).

However, the reasons for this variation in calf survival from year to year are not so clear.

Various attempts were made to correlate survival (or conversely mortality) to rainfall. Rainfall is obviously the major factor which will influence or determine habitat conditions from year to year and it can be safely assumed that habitat condition is the prime proximate factor influencing mortality and/or survival rates in any population. Given optimum habitat conditions, any population could be expected to grow, while the further habitat conditions depart from the optimum, the greater would be the effect on survival. Table 4.3.25 gives the cow/calf ratios from respective cohorts when each was one year old (January count) and also the rainfall from the particular rainy season concerned. No relationship could be shown to exist.

Table 4.3.25: Wildebeest cow/calf ratios from respective cohorts and annual rainfall figures from the Central District of the Kruger National Park between 1977 and 1983

Year of birth	Calves per 100 cows at one year old	Rainy Season*	Annual rainfall**
1977	24,0	1976/77	742,8
1978	40,1	1977/78	429,1
1979	50,9	1978/79	611,5
1980	57,6	1979/80	817,5
1981	60,1	1980/81	393,5
1982	53,8	1981/82	307,9
1983	32,6	1982/83	553,5

* Rainfall measured from July to the following June from respective rainy seasons.

** Rainfall averaged from the four Central District Stations Satara, Kingfisherspruit, Nwanedzi and Tshokwane.

The possible influence of the previous year's rainfall on calf survival was also examined as this would largely have determined the habitat conditions prevalent during the calving season. For each calf cohort, rainfall from the season prior to birth and that from the first year of life were averaged and plotted against cow/calf ratios at one year old but this relationship was also not significant.

From Table 4.3.22 and Figure 4.3.13 it is obvious that initial mortality is also highly variable (initial mortality here refers to the number of calves dying between birth and the first count in January). From the January counts cow/calf ratios differed between 52,4 and 80,4 calves per 100 cows. Although no data were gathered on pregnancy rates during this study, other author's have produced no evidence to suggest that pregnancy rates in adult wildebeest cows may vary from year to year (Attwell, 1978; Attwell & Hanks, 1980; Braack, 1973). Braack (1973) however, found that pregnancy rates varied among yearlings (11,8% in 1967 and 57,1% in 1972) but the percentage of yearlings in the population is small (between 9,5% and 15,5% at 21 months) and half of these can be expected to be male and thus the variation in pregnancy rates in this age class would not exceed the variation observed in cow/calf ratios in January. It must therefore be the mortality rates which vary and not the pregnancy rates.

The difficulty in correlating calf and/or yearling survival rates to rainfall is probably because the effect of rain is far more complex than merely a single figure which indicates the amount of rain that has fallen. Firstly there are only four rainfall stations in the CD and, as most of the rainfall is in the form of thunderstorms and are therefore largely localised, the averaged rainfall data is unlikely to be representative of the actual rainfall in all parts of the CD. Also the time of year that rain falls, the type of rain, the amount of run-off and the amount of grass cover present (which reduces evaporation from the soil) are examples of the factors which influence the effect of the rain. These factors in turn influence the response of the habitat to the rainfall.

It is probable that some measure of habitat condition related to rainfall (e.g. standing crop, lateral visibility or grass length) would provide much closer correlations than the rainfall data itself, but unfortunately no such data were collected during this study.

Data collected during ground counts (e.g. cow/calf ratios) proved to have little or no predictive value in terms of actual population trends. Attempts to correlate such data to the percentage increase of the population were unsuccessful.

Only the combined total of the July cow/calf and cow/yearling ratios showed any significant correlation when plotted against the percentage increase or decrease of the population over the past year. Population estimates are obtained annually from aerial surveys in July and therefore the ratios from July grounds gave the closest correlations as could be expected.

Table 4.3.26 gives the cow/calf plus cow/yearling ratios and the increase or decrease in the population.

Table 4.3.26: Combined cow/calf and cow/yearling ratios from July ground counts and the annual percentage increase or decrease in the wildebeest population of the Central District of the Kruger National Park between 1979 and 1983

Year*	Combined cow/calf and cow/yearling ratios	% increase or decrease in population
1979	76,9	- 7,3
1980	86,8	+ 22,0
1981	85,4	+ 12,0
1983	69,6	- 6,7

* Ground counts were not conducted during the months of July during 1978 or 1982 thus only four data points are available.

Figure 4.3.13 shows the least squares regression-line fitted to these data which is described by the equation y = 77,2 + 0,5 x. The implication is that the smaller the combined cow/calf plus cow/yearling ratios, the smaller is the percentage increase in the population for that year. However, a point is reached where population growth is negative and below this point the population actually declines. The line fitted to the data indicates this point to be at a combined cow/calf and cow/yearling ratio of 77,2. Therefore, if July ground counts yield a combined cow/calf plus cow/yearling ratio of greater than ± 77, an increase can be expected in the population while ratios lower than this would suggest a decline.

The biological significance of this is that both the calf and yearling survival rates need to exceed a certain minimum before the population will show an increase. A high yearling mortality may negate population growth even though calf survival is high and vice versa.

One last aspect of interest emerged from the cow/calf and cow/yearling ratios. A closer inspection of Figure 4.3.12 (page 149) showed that each respective calf crop followed the same pattern of mortality from birth to 21 months old. There was an initial steep decline from January to April or July followed by a leveling off until the following October. This was followed by another steep decline to around July which was followed by an actual increase in the final October count. To confirm this pattern, totals of cows and calves (from Table 4.3.22) for counts from each respective month after birth for each calf cohort were pooled to give a mean cow/calf or cow/yearling ratio for that time of year. These averages are given in Table 4.3.27 as are results of the chi-squared tests where each count's cow/calf ratio is tested against its predecessor. The trend is shown graphically in Figure 4.3.14.

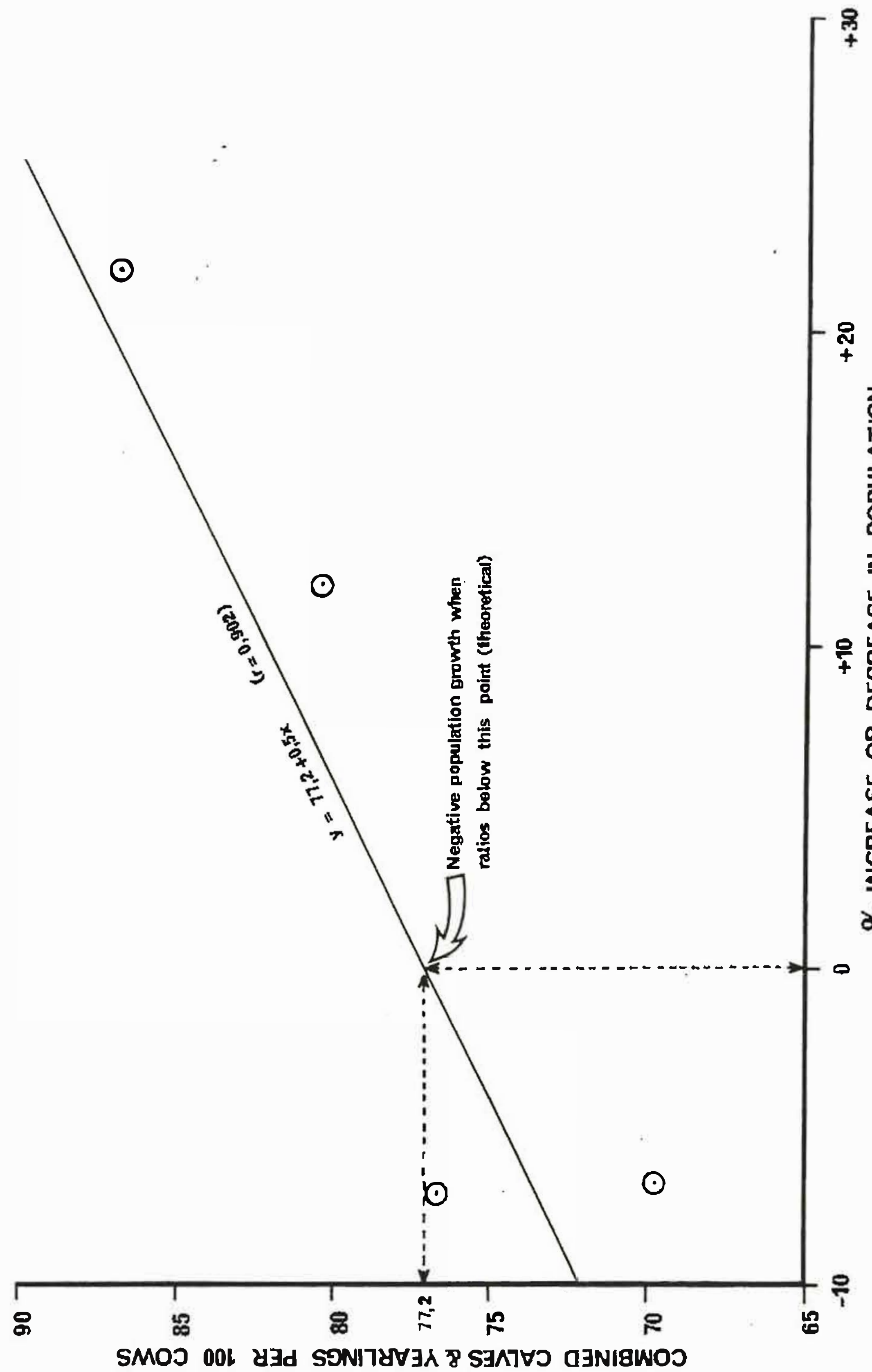


FIGURE 4.3.13: The relationship between combined cow/calf and cow/yearling ratios in July and the population trend calculated from aerial survey data (also collected in July) in the wildebeest population of the Central District of the Kruger National Park.

Table 4.3.27: The total number of wildebeest cows and calves or yearlings from ground counts conducted at the same times after birth for respective calf cohorts from the Central District of the Kruger National Park between 1978 and 1984.

Month of counts	No. of count after birth	No. of counts	Total no. of cows*	Total no. of calves*	Chi-sq. test**	χ^2 value	p	Calves per 100 cows
Jan.	0	7	3 935	2 695	-	-	-	68,49
Apr.	1	6	3 587	2 088	0 vs. 1	18,96	<0,001	58,21
Jul.	2	4	2 694	1 481	1 vs. 2	1,76	>0,1	54,97
Oct.	3	6	3 410	1 836	2 vs. 3	0,21	>0,5	53,84
Jan.	4	7	3 935	1 836	3 vs. 4	12,39	<0,001	46,66
Apr.	5	6	3 587	1 252	4 vs. 5	44,74	<0,001	34,90
Jul.	6	4	2 694	655	5 vs. 6	43,83	<0,001	24,31
Oct.	7	6	3 410	970	6 vs. 7	7,50	<0,01	28,45

* These columns give the total number of cows or calves counted during respective counts e.g. the 3 935 cows in the top row is the total number of cows counted during all January counts.

** This column gives the rows tested against each other (from the number of the count after birth given in column two of the table).

The pattern clearly emerges from these ratios. There was an initial significant decline between the January and April counts which levelled off for the next two counts with insignificant differences between them. This was followed by a second period of decline for the next three counts, each significantly lower than its predecessor. Lastly there was a significant <u>increase</u> in the cow/yearling ratio up to the final October count. For illustrative purposes a fourth order polynomial was fitted to the data points in Figure 4.3.14. The equation is given here as it may be useful for future comparisons:

$$y = B_0 + B_1X + B_2X^2 + B_3X^3 + B_4X^4$$

where $B_0 = 68{,}7125$

$B_1 = -21{,}0075$

$B_2 = 12{,}5729$

$B_3 = -3{,}10322$

$B_4 = 0{,}231137$

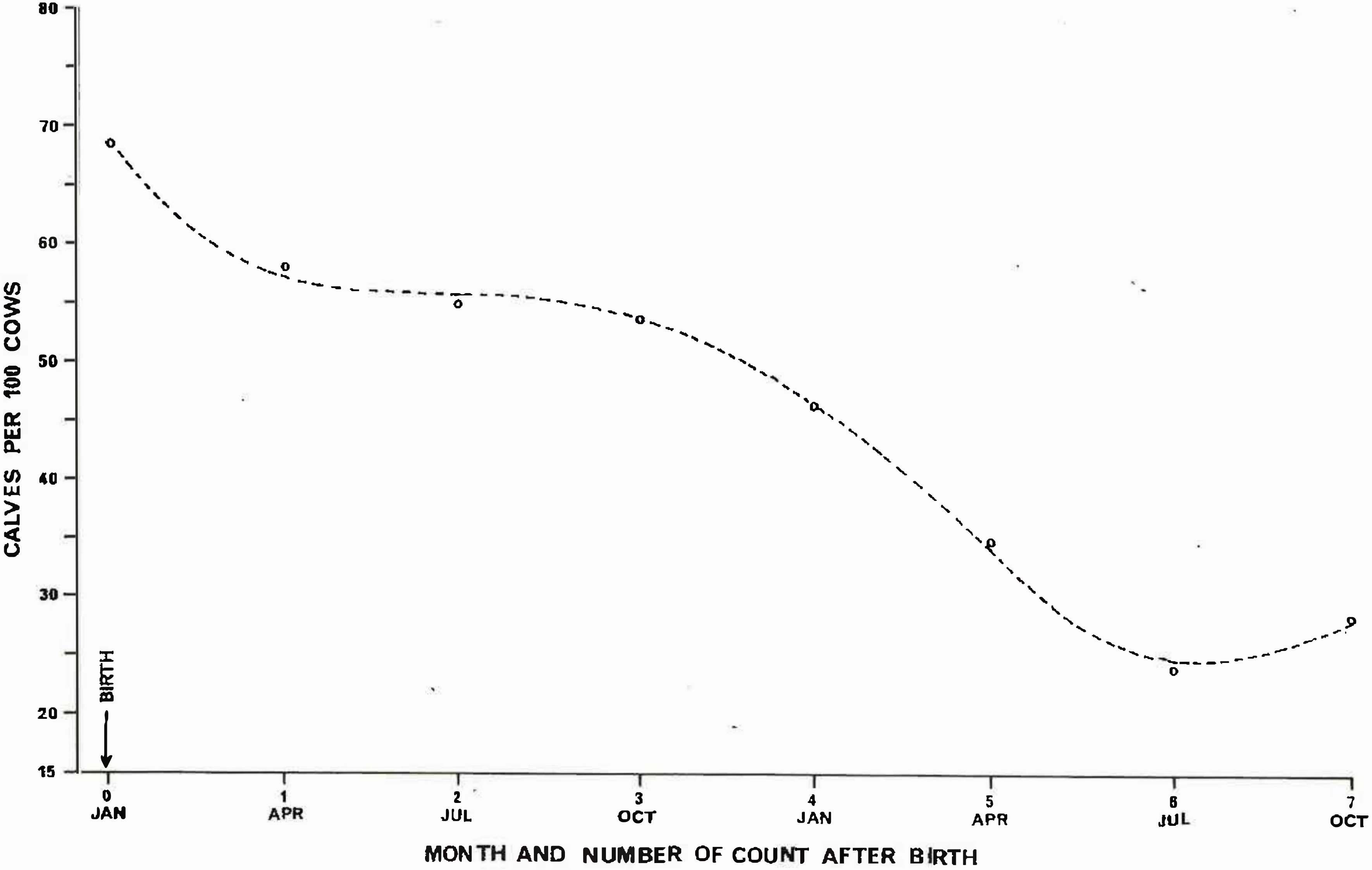


FIGURE 4.3.14: The pattern of wildebeest calf mortality from birth until 21 months of age in the Central District of the Kruger National Park.

Once again it need be stressed that these counts could in no way indicate adult mortality and that calf mortality can also only be inferred from the decline in the proportion calves to adult cows over time.

The pattern illustrated by the curve in Figure 4.3.14 was consistent in <u>every</u> calf cohort which was sampled over the full period from birth to 21 months old. Calf cohorts born in 1978, 1979, 1980 and 1982 showed an increase in their proportion to adult cows in the final count, while the cohort born in 1982 had actually increased above ratio measured in the April count six months earlier (see Table 4.3.22). The only way that the proportion of yearlings can increase in such a ratio, is that the number of adult cows must have decreased in proportion. This suggests that there is an increase in mortality among adult cows between the counts of July and October (the end of the winter). This mortality was not reflected in the ratios when calves were a year younger and were still only six to nine months old and this must be due to the fact that calves of that age are still dependent on their mothers and thus, if the cow dies the calf will almost certainly also die. If both cow and calf die, this would not affect the ratio of the sample, while a year later when the yearlings are 18 to 21 months old, death of the mother would not necessarily also mean the death of the now independent yearling. This differential mortality would result in the increase in the proportion of yearlings in the sample.

From the trends in Figure 4.3.14, calf mortality is high in the late summer and early winter months (from January to July) in both of the calves first two years of life as this is when the most significant decline occurs in the cow/calf ratios of respective cohorts. Therefore there are temporal differences in mortality rates between cows and calves or yearlings - calves and yearlings experiencing their heaviest mortality between January and July while adult cows experience theirs between July and October.

This phenomenon only became evident during the analysis of the data and thus the reasons for its occurrence were not investigated during field work. There is therefore no further evidence in its support, but the high χ^2 values (Table 4.3.24) and the consistency of its occurrence from cohort to cohort leave little doubt that these trends do occur. The factors inducing this phenomenon however, are at this stage still unknown.

4.4 CONCLUSIONS

4.4.1 Marked animals and movement

The main reason for the marking of wildebeest was to reaffirm or refute the "sub-population theory" (Braack 1973; Smuts, 1972). Confirmation that movement patterns had not changed markedly would validate the separate analysis of sub-population data particularly with regard to sub-population trends, as an understanding of the sub-population trends during the period of the population decline could obviously give an insight into the reasons for the decline itself. In this, the marking programme would appear to have been successful as only three of the marked animals were ever recorded to cross the rather arbitrary boundaries ascribed to the three sub-populations' areas. All of these three animals crossed the boundary between the Satara and the Sweni/Mlondozi sub-population and no movement was recorded over either of the other boundaries. Aerial survey data extracted per sub-population supports not only this, but also the actual placing of the sub-population boundaries, as a clear picture of the declines (and subsequent increases) in the respective sub-populations emerges (anomalies in the trend may suggest misplaced sub-population boundaries). Towards the end of the study period however (1983 and 1984), the data also confirm that there was some movement across the boundary from the Satara to the Sweni/Mlondozi sub-population in 1983 and back again in 1984. Although this could not be substantiated by the movement of marked animals it is clearly unreasonable to assume that <u>no</u> movement takes place. The boundary is arbitrarily defined for the computer and the Sweni River itself is by no means an absolute physical barrier. Although northern (Satara) and southern (Sweni/Mlondozi) sub-populations occur on the eastern half of the CD, suitable wildebeest habitat is continuous (the basalts - see Figure 2.3.1) and no barrier, either physical or habitat related, separates them, and a certain amount of crossing is therefore inevitable. Fires close to this boundary could particularly be expected to lure wildebeest and other herbivores across such a boundary.

The same is not true for the boundaries between both the Satara and the Western Boundary, as well as the Sweni/Mlondozi and the Western Boundary sub-populations respectively. No evidence of movement across either of these boundaries was obtained and this is almost certainly ascribable to the dense belt of <u>Acacia welwitschii</u> thickets growing on Karoo sediments (Figures 2.3.1 and 2.5.1) which present a fairly stringent faunal barrier to plains-loving wildebeest. Smuts (1972; 1974b) also did not record any movement of marked zebra across this boundary.

From this evidence it is obviously legitimate to analyse the sub-population data separately, and although movements may influence sub-population trends over short-term periods, boundaries appear to be placed accurately enough to monitor long-term trends satisfactorily.

4.4.2 Population and sub-population trends

Confirmation of the validity of ascribing discrete areas to the three sub-populations, the detailed recording by Pienaar (1965) of numbers and localities of wildebeest recorded during that year's aerial census and the modern method of aerial ecological surveying, have all made it possible to establish clearly the trends followed by the three sub-populations since 1965. This has given valuable insights into the reasons for the decline and allowed an appraisal of some previously proposed explanations for its occurrence.

a) Disease and parasites. The hypothesis that the population decline may have been caused by diseases and parasites (Horak et al., 1983) prompted an investigation into wildebeest parasite loads. They concluded, however, that "Although numerous species of parasites were recovered ... the magnitudes of the burdens were such that they produced no readily detectable pathological changes; thus it did not appear as if parasites were the cause of the decline in the wildebeest numbers".

b) Provision of artificial water. This theory held two main tenets (Smuts, 1976b). The first was that artificial water points held back and thus disrupted the wildebeest migration, while the second held that water points placed in areas where no permanent water was previously available, allowed the build-up of water dependent large herbivore communities around the waterpoint. This in turn allowed the establishment of permanent lion prides. The theory also held that wildebeest use migration to escape predators but subsequent to the establishment of permanent lion prides in all areas of the Central District, escape was no longer possible and with a larger number of lion prides preying on the population, it was forced into a decline.

This explanation is unlikely, because although 105 waterholes and dams have been systematically provided throughout the CD, the traditional migratory pattern still persists in the Sweni/ Mlondozi sub-population and this sub-population has in fact recovered since the nadir in the cycle in 1980.

c) Wildebeest culling. Wildebeest culling, which was initiated in 1965, continued after 1969 and thus into the period of the decline. Culling an already declining population was supposedly enough to have forced the population into an even steeper decline and to a lower point than would naturally have been the case (Smuts, 1975b). Culling figures are given in Table 4.4.1.

Of these wildebeest culled, however, 2 303 (73%) were culled before the decline started and it seems unlikely that the culling of the remainder (852) from a population of 13 950 could have instigated such a drastic decline.

Table 4.4.1: Population estimates and culling quotas for wildebeest in the Central District of the Kruger National Park between 1965 and 1971 (culling figures obtained from Smuts (1972)).

YEAR	POPULATION ESTIMATE	NO CULLED
1965	12 197	164
1966	-	392
1967	-	852
1968	13 130	368
1969	13 950	527
1970	11 838	550
1971	10 650	302
TOTAL		3 155*

* In addition to these, 78 were shot for research purposes in 1972 (Braack, 1972) and 55 more in 1977/78 for Veterinary Research (Horak, de Vos & Brown, 1983).

d) The above average rainfall cycle between 1970 and 1980. This theory (Joubert et al., 1974) also held two main tenets of which the first was habitat change - which was later shown to have taken place in the CD (Coetzee, Gertenbach & Nel, 1976) - the rank conditions being unsuitable for wildebeest. The second tenet was increased predation. This tenet went hand-in-hand with the previous one - the structural changes in the vegetation rendered wildebeest more vulnerable to predators due to an increase in cover.

Much circumstantial support for this comes from Stevenson-Hamilton's early reports of population trends when these are evaluated in the light of the wet and dry climatic cycles which have now been shown to exist by Tyson & Dyer (1975) and Gertenbach (1980a). They have shown that these cycles conform roughly to a 20 year oscillation consisting of 10 years of above, followed by 10 years of below average rainfall. Hall (1976) suggests from dendroclimatological studies that this 20-year oscillation has persisted since as far back as 1750. Tyson and Dyer (1978) found that there was a change in phase around the beginning of this century when a double dry spell occurred from 1897 to 1915. It was during this time (1902) that Stevenson Hamilton came to the Sabi Game Reserve and he reported that between 1902 and 1916 "all species had increased" (Stevenson-Hamilton, 1939). In this same article he states that between 1916 and 1924, "wildebeest had died during the rains". These periods conform exactly to the first of the recorded dry and subsequent wet cycles (see Figure 2.2.3). He goes on to say that between 1923 and 1932 (dry cycle) there had been a "rapid and uninterrupted increase in their (wildebeest) numbers", while from 1932 to 1939 (wet cycle) there had once again been a "visible decline in numbers". Over the next 14 years the population had decreased (Steyn 1953) which although this had occurred mainly during the following dry cycle, was ascribed to their being afforded no protection from hunters during their movements to areas outside the CD (Stevenson-Hamilton, 1942)and to the "increase in the bush" (Steyn 1953). The increase in the bush can largely be ascribed to the changes in the burning policy instituted by Sandenbergh in 1946 who was against any form of deliberate veld burning (Gertenbach, 1984). The burning policy was changed again in 1954 and blocks were subsequently burned every three years. This fire regime, in spite of the wet cycle (which was very moderate with no excessively wet or dry years), appeared to favour wildebeest as Anonymous (1961) reported that "* the wildebeest numbers of the Central District are still increasing". The western boundary fence was erected in 1961 and the subsequent history of the CD wildebeest population have been discussed at length, but it can be seen that up to the time of the change of the burning policy by Sandenbergh, the subjective impressions of Stevenson-Hamilton which indicated population increases and decreases, coincided almost exactly with rainfall cycles of which he could not even have been aware. The more recent and drastic decline between 1970 and 1979 also coincides almost exactly with the period of the wet cycle from 1970 to 1980

(Gertenbach, 1980a), and with the onset of the subsequent dry cycle there was an immediate concomitant recovery of the population. All three of the sub-populations underwent declines during the decline phase of the population during this wet cycle but subsequently, only the Satara and Sweni/ Mlondozi sub-populations have shown any marked degree of recovery. In fact, these two sub-populations followed almost exactly the same trends which suggests that the same factors which induced the decline acted on both of these sub-populations in the same manner. The Western Boundary sub-population however, underwent a far more serious decline and has shown only a very minor recovery. This suggests that there was an additional factor which helped to reduce this sub-population which was not acting on the other two. The only remaining possibility is the severing of the Western Boundary sub-population's migration routes by the western boundary fences.

The conclusions drawn are that long-term weather cycles do occur in the KNP, and probably have done for centuries, and it can be expected that the wildebeest population is adapted to them and will always fluctuate in accordance with these cycles. More specifically that wetter cycles induce population declines while drier cycles are more favourable and allow a recovery. The 1970-1980 wet cycle was an exceedingly wet period and its effect on the wildebeest was probably also above average and therefore future, more normal cycles may not affect the population so drastically. However, this wet cycle was not the only factor inducing the decline as the western boundary fences also played an extremely important role - possibly with irretrievable effects.

4.4.3. The effects of fencing on the wildebeest population

Section 4.3.2 of this chapter has shown that the Satara and Sweni/Mlondozi sub-populations underwent declines during the wet cycle which occurred from 1970 to 1980, but have subsequently recovered to levels exceeding those obtained during the first aerial census in 1965. The Western Boundary sub-population on the other hand, also declined over the same period but failed to recover and has now stabilised at a new level of around 1 500.

Although various management practices (e.g. wildebeest culling or provision of artificial waterpoints) may have affected the ecology of these three sub-populations, these were applied to all three of the sub-populations and can therefore not account for the failure of the Western Boundary sub-population to recover as did the other two. The only disruptive factors which affected only the Western Boundary sub-population were the severing of migration routes and the excision of summer grazing areas by the western boundary fences and these were enough to compel this sub-population into a decline of around 90%, from which it has not recovered.

Although these were certainly the proximate factors inducing the decline, the ultimate mortality factors were far more discrete. Reports by Adendorff (1984) and Anonymous (1963) indicate that mortalities did occur initially but once the herds had become accustomed to the barrier, no more mortalities resulting directly from the fences were reported. However, the decline in this sub-population continued as has now been shown from aerial census data, and in spite of this, no reports of excessive mortalities were received. This means that this sub-population had gradually "wasted away" as the reduced area of less suitable habitat could not support its previous numbers. Having now lost the prime objective for migrating - the summer grazing area - the migratory status of this sub-population has been altered and now consists of small sedentary herds occupying islands of suitable habitat on the seeplines and gabbro patches in the area. Having thus also lost the instinct to migrate, and probably existing now at the carrying capacity of their new island habitats, it is unlikely that this sub-population will ever increase to a point where a migratory urge may be invoked, and therefore, even if the western boundary fence were to be removed, it is unlikely that this sub-population will ever regain its former numbers or migratory way of life.

Other areas' wildebeest populations have also experienced delines as a result of fencing. Berry (1980a; 1980b) reported that fencing and anthrax had resulted in population declines in Etosha, while Owen & Owen (1980) and Williamson & Williamson (1985) have reported on the drastic effects of the veterinary fences on the migratory wildebeest herds in Botswana.

I conclude, therefore, that while the 1970 - 1980 wet cycle contributed to the decline, the population of the CD has already recovered from its effects, and that the lowered population level now prevailing in the CD is as a direct result of the population crash which was induced in the Western Boundary sub-population by the two fences erected for veterinary control measures and for the protection of the Orpen area against over-grazing.

4.4.4 Population structure

4.4.4.1 Adult sex ratio

Although the distortion in the adult sex ratio has been adequately described, the reasons for it could not be identified during this study and can only be speculated on here.

From Figure 4.3.11 and Table 4.3.18 it was shown that distortion was as a result of an increasing number of bulls and a concomitant decreasing number of cows in the population and this could have been caused either by one or more calf cohorts with skewed initial sex ratios at birth moving into the adult age classes, or by increased cow mortality and/or aproportional bull survival.

For the former possibility it is unfortunate that no foetal, calf or yearling sex ratio data could be collected during this study and thus the potential contribution of initial sex-ratio differences could not be determined. However, such skewed ratios among foetuses and calves have been described for various species such as Scandinavian moose (Alces alces (Reuterwall, 1981); the genus Odocoileus (Verme, 1983); and buffalo (Whyte, Pienaar & Vos, 1984; Whyte, in prep.) and the possibility of this happening in wildebeest cannot be excluded. Whyte (in prep.) found that skewed foetal and post-natal sex ratios in buffalo were probably due to drought conditions in the northern areas of the KNP under which the distortion was in favour of females (40 males : 67 females: χ^2 = 6,81; $p<0,01$). In the southern areas of the KNP were rainfall had been good, there was no distortion (90 males : 83 females; χ^2 = 0,28; $p>0,5$). Should wildebeest foetal sex ratios also be affected by adverse climatic regimes, the distortion would appear to be in favour of males during wetter conditions.

Estes (1969) concluded that immature bulls inevitably end up in bachelor herds and as abnormally large bachelor herds were recorded during this study while the cow:bull ratio was at its lowest, this adds to the evidence that skewed foetal, calf or yearling sex ratios may have played a role in the distortion of the adult sex ratio when they moved into the adult age classes.

The second possibility, that there was an increased cow mortality and/or a decreased bull mortality brings to mind that it could have been caused by lion culling in the summer grazing area of the Sweni/ Mlondozi sub-population (see Figure 4.1.1.) as a large proportion of the bulls stayed behind on their territories in relatively predator-free conditions while the females moved south and were exposed to normal predator pressures resulting in greater female mortality.

But, if in fact lion cropping had been responsible for the distortion in the sex ratio it would be expected that the distortion would be evident in only this sub-population. The majority of the distortion, however, took place in the Satara sub-population and not in the Sweni/Mlondozi sub-population as expected. The Sweni/Mlondozi sub-population did show a similar trend but was not nearly as dramatic. The Western Boundary sub-population on the other hand showed marked variability and no discernible trend. The proportion of cows to bulls in this sub-population was consistently higher than in the other two intimating a higher mortality rate amongst bulls. It is clear however that lion cropping could not be held responsible for the distortion in either the population's or either sub-populations' sex ratio. Further effects of lion culling will be discussed in Chapter 5.

The consistently higher proportion of cows per bull in the Western Boundary sub-population deserves some discussion. The reason for this is almost certainly due to a greater mortality rate among the bulls which must be related to the now sedentary nature of that population and the nature of its habitat. This sub-population is limited to island-like patches of suitable habitat scattered throughout the landscapes to the east of the Karoo sediments. Most of the larger patches or "seeplines" support sedentary herds of wildebeest and each constitutes a suitable territory for an adult bull. Territorial bulls are intolerant of bachelors which are forced into the less suitable parts of the habitat (Estes, 1969) and this would lead to a greater mortality than among breeding herds which are sedentary on the patches of optimum habitat.

4.4.4.2 Cow/calf and cow/yearling ratios

Although it has been shown from ground count data that considerable variation exists in the survival/mortality rates of wildebeest calves and yearlings from year to year, it was found that the cow/calf and cow/yearling ratios only have a moderate measure of predictive value in the determination of population trends. From the rather sparse data it was shown that the sum of the cow/calf and cow/yearling ratios determined during July at which time the aerial surveys were also conducted correlated fairly well with the percentage increase or decrease in the population during that year. However, it is not only recruitment of juveniles which will determine the trend in the population and adult mortality, for which there is no absolute measure from ground counts, obviously plays as important a role as recruitment and thus combined cow/calf and cow/yearling ratios cannot in themselves be entirely accurate for predictive purposes. Also, due to the many factors which influence the effect of the rainfall on the habitat, and to the small number of rainfall stations in the CD, no satisfactory relationships could be shown to exist between rainfall and calf and/or yearling survival rates.

I had hoped that a useful predictive mathematical model could be developed based on these ratios, but for the reasons mentioned above, this has not been possible. However, the subjective impression gained during field work was that if and when conditions in the field layer are exceedingly long and rank due to prevailing above-average rainfall over an extended period, not only calf mortality, but mortality in all segments of the population can be expected to be high leading to lowered or even negative population growth. On the other hand, during "normal" climatic regimes which lead to more open vegetation conditions which favour wildebeest, mortality will be reduced and population growth may be very great as can be seen from the 24% growth recorded between 1981 and 1982.

However, extreme drought conditions do also not favour wildebeest and can lead to very high calf mortality. This was observed during the summer of 1982/83 and in particular during the January 1983 count when drought conditions in the CD were at their worst and many wildebeest were noted to be in poor condition (the only time during this study) and cow/calf ratios were the lowest recorded in any January count during the study.

CHAPTER 5

THE LION-WILDEBEEST PREDATOR-PREY RELATIONSHIP

5.1 INTRODUCTION

The concern for the wildebeest population which had showed a persistent decline since 1970 led eventually to a predator cropping campaign whose main objective was to relieve predator pressure on the wildebeest population in their summer grazing grounds during the calving period. This in turn gave rise to population structure analyses of the wildebeest population from ground count data which was one of the main thrusts of this research project. Results of these analyses were presented in the previous chapter, but will also receive further attention in this chapter in an evaluation of the success of lion cropping in terms of calf survival rates.

The implication of lions in the wildebeest population decline prompted the inclusion of the lion-wildebeest predator-prey relationship in this study. Predator-prey relationships are exceedingly complex however, and in an ecosystem like the CD where a full range of predators occurs, preying on a wide spectrum of potential prey species, the relationships and interrelationships of predators, prey and the environment in the food web become so complex that they probably defy complete understanding. A prey animal is caught by a predator due to vulnerability to the capture methods of the predator concerned. This vulnerability may be either momentarily (e.g. from having its head down to drink) or for longer or even extended periods of time (e.g. as a result of habitat change due to prevailing climatic conditions). Factors affecting the vulnerability of a prey individual to one or more of its predators therefore vary from extreme debilitation due to starvation and/or disease on one end of the scale through to momentary vulnerability of an otherwise prime individual at the other. Temporary vulnerability represents an opportunistic possibility of a kill to a predator and thus the population dynamics of the prey species involved would not be affected to any significant degree, while vulnerability induced by habitat change is more general in its effect and may result in a decline in a population of the prey species concerned. A complete understanding of such a predator-prey relationship would entail an appreciation of why a prey animal had become vulnerable to its predator and whether the condition was temporary or of a less transient nature.

There is a host of literature on the subject of lions related to all aspects of their ecology and much of this literature is concerned with various aspects of their predator-prey relationships with various prey species. These authors include Bertram (1978), Bryden (1976), Elliot and McTaggart Cowan (1978), Eloff (1964), Guggisberg (1961), Hirst (1969), Pienaar (1969b), Rudnai (1973), Schaller (1972), Smuts (1975b, 1976b, 1978b, 1978c), Stevenson-Hamilton (quoted in Pienaar, 1969b), Talbot & Talbot (1963), Van Orsdol (1984) and Wright (1960).

A review of all this literature would be unnecessarily time and space consuming and it should suffice to say that all of these authors have attempted in some way or another to determine the nutritional requirements of lions, the number of animals they kill, the frequency at which kills are made or their impact on one or more prey species. Data used for these calculations have been obtained by various means and these include direct observation of single prides for varying lengths of time (Bertram, 1978; Bryden, 1976; Schaller, 1972), diurnal tracking of lions in sandy environments using expert bushman trackers to locate and identify kills (Eloff, 1964), the use of extensive, long term routine patrols to locate kills (Hirst, 1969; Pienaar, 1969b; Smuts 1978b) while other studies have used telemetry to track prides as often as possible with the hope of locating kills (Bryden, 1976). But during the course of this study it became apparent that all of these calculations have relied heavily on extensive assumptions and arbitrary extrapolations in order to arrive at a conclusion, which leaves the feeling that the questions have largely remained unanswered. In this respect the radio telemetry study of lions described here has proved to be no exception. The objective of this portion of the study was to assess the impact of lions on the wildebeest population, and the question ultimately to be answered is: Is lion predation potentially capable of limiting - or in unfavourable habitat conditions (as during wet cycles) - of actually reducing the wildebeest population? The calculations given in this chapter are also necessarily based on assumptions and extrapolations which may or may not be valid. This is unavoidable as it is obviously not possible to monitor all prides at all times in order to locate all kills or to have continuous and accurate census data of the prey available to these prides to make the necessary comparisons between the kill data and the prey available. However, in this chapter the data are given and where assumptions have been made for extrapolative purposes, attention has been drawn to them.

The complexity of the predator-prey food web in a system like the CD obviously renders an attempt at comprehensive analysis in a treatise such as this impossible and therefore only a few aspects have been selected and these form the basis of this chapter.

5.2 METHODS

5.2.1 Rangers' returns

Section Rangers in the KNP are required to submit a monthly return of all kills recorded on their sections. These returns record the predator species responsible and also the species, sex and age (if known) of the prey. Only kills which can be assigned to a particular predator species with reasonable certainty are supposed to be recorded (Pienaar, 1969b).

The CD is at present made up of five complete Rangers' Sections - Tshokwane, Satara, Nwanedzi, Kingfisherspruit and Houtbosch-rand. Two others however, Olifants and Lower Sabie have portions of their areas within the CD. The Lower Sabie section extends south of the Sabie River into the Southern District while the Olifants section extends to the north of the Olifants River. In both of these sections, no distinction was made in the kill returns between animals killed inside or outside the CD and the data from these two sections were therefore excluded from the analysis.

Analysis of the data was conducted according to the method of Pienaar (1969b) which was also used later by Smuts (1975b). This entails the calculation of the relative abundance of the various prey species available to the predator from census totals and the calculation of the relative frequency at which the various prey species are killed by predators from the Section Rangers' kill returns. A "preference rating" for each prey species can then be calculated by:

$$\text{Preference rating} = \frac{\text{Relative frequency in prey sample}}{\text{Relative abundance in prey community}}$$

Thus this rating or "index" takes cognizance not only of the proportion that each prey species contributes to the particular predators diet, but of its availability to the predator as well and thus gives a useful insight into its vulnerability to the predator. It is, however, dependant upon accurate census totals and reliable kill data reflecting the actual proportion in which each prey species is taken by the predator. Kill data are collected by Rangers themselves and also by their field staff during routine patrols of their respective areas. This method of data collection has some inherent biases as smaller species are under-represented due to the remains of such a kill being more difficult to locate. Remains from a smaller kill are not sufficient to attract vultures in any numbers as these are sometimes consumed totally by the predator and as it is usually the activity of vultures which indicate kills to the field staff, smaller kills have a reduced probability of being found. This is proven by the fact that impala are consistently lowest in the preference ratings calculated by this method, yet in a sample of 252 culled lions' stomachs, 40 contained impala - more than any other of the prey species (Smuts, 1978 b, c). The same also applies to the young of larger species and calves are obviously under-represented in these samples even though it is known that initial calf mortality is fairly high (e.g. for wildebeest - see previous chapter). However, if it is assumed that the proportion of found kills of respective species remains much the same from year to year, then changes in the preference ratings over time probably indicate a shift in predator vulnerability from one prey species to another.

Census data were obtained from annual ecological aerial surveys and the same assumptions are made regarding these totals - i.e. that a constant proportion of the population of each respective species is counted each year, and that although the census total may not accurately reflect the actual population total, increases or decreases from one census to the next will indicate actual population trends, and that the relative frequencies of prey species available to the predator will therefore change accordingly for the purposes of the calculation of preference ratings.

Results of these analyses should therefore be evaluated with these assumptions, biases and limitations in mind.

5.2.2 Found wildebeest skulls

During all aspects of field work, wildebeest skulls were collected routinely. From these skulls age at death was estimated according to the method of Attwell (1980) while sex was determined by the sexually dimorphic horn development characteristics (see Chapter 4). Although horny tissue had often been removed from the older skulls by infestations of larvae of the moth *Ceratophaga vastella*, the underlying bony tissue of the horns was still found to be adequate for the purposes of sex determination from the skull.

Found skulls were assigned to arbitrary age classes (age here referring to the time lapse since the death of the animal). Eight classes could be distinguished and these were:

1. Fresh - a day or two after death
2. Less fresh but hair, skin and flesh still attached.
3. No hair, skin or flesh still attached but no sign yet of decomposition of the bony material (No C. vastella larvae on horns).
4. First signs of decomposition of the horn tissue.
5. Decomposition of the horn tissue well-advanced.
6. Horn tissue almost completely decomposed.
7. No horn tissue left but bony structure still well-preserved.
8. Bone of skull brittle and crumbly - decomposition far advanced.

Two things should be kept in mind with the analysis of the data from these skulls. These are (a) that the time intervals between classes are not equal and are in fact unknown, but circumstantial observations suggest that hair, skin and meat have been removed from the skull at about two months and that horny tissue has disappeared at about two years and (b) that although these age classes were assigned as and when the skull was found, they were all reclassified once the skull sample was complete. If this had not been done a fresh skull in 1982 would fall into the same age class as a fresh skull in 1984 which would invalidate the analyses if it were intended to compare the data from different time periods. Skulls were therefore all re-assigned to these age classes early in 1984 in order to maintain the chronological sequence of the time of death of the whole skull sample.

Not all of the 246 skulls found could be used for both sex and age determination. Sex could be determined in all cases while age could only be determined in 173 due to the disappearance of the teeth.

Although it is known that other predators also take wildebeest (Pienaar, 1969b; Kruuk, 1972; Mills, 1984), Pienaar (1968b) estimated that 97,7% of wildebeest kills in the KNP were made by lions. Apart from predation, no other mortality factors are known to have significantly affected the wildebeest population of the CD in the recent past. The western boundary fence was known to have directly caused some mortalities (Adendorff, 1984) and to have been the indirect cause of the decline in that sub-population, but of the total skull collection (n = 246), 95,7% were found in the other two sub-population areas which were unaffected by the fence. For these reasons, and for the purposes of this study, all of the skulls found were considered to have come from wildebeest killed by lions.

5.2.3. Condition of wildebeest killed by lions

Although Berry (1980a) could usually distinguish five categories of physical condition in the wildebeest of the Etosha National Park, it was only for a short time during the study period that some of the wildebeest of the CD could have been classified as anything less than "fair" (Berry's condition class 3). This was during the early summer of 1982/83 when the drought of the previous year persisted due to the non-arrival of the early summer rains and consequently grazing was particularly scarce. Up until this time, which was close to the termination of the study, the persistent "good" condition of the wildebeest in the population had obviated any necessity to make visual estimates of physical condition. However, as physical condition may represent a measure of an animal's vulnerability to predation, it was felt that an estimate of physical condition of wildebeest killed by lions may provide further insights into this specific predator-prey relationship.

A wide variety of methods for the assessment of condition of mammals have been described (see Hanks, (1981)), but for the obvious reason that lion kills are almost totally consumed, it was not possible to use most of these (e.g. kidney fat index (KFI) or packed cell volume (PCV) of the blood). However, as the long bones of such kills are nearly always available after the departure of the lions, marrow samples were available for the estimation of bone marrow fat (BMF).

As in other ungulates, wildebeest BMF has been shown to have a close correlation to the percentage dry mass of the marrow. Earlier investigations have produced very similar regression equations describing this relationship ($y = 1{,}0047x - 5{,}76$: $r = 0{,}998$ (Attwell, 1978); $y = 1{,}0x - 6{,}43$: $r = 0{,}997$ (Brooks, Hanks & Ludbrook, 1977); $y = 1{,}0042x - 7{,}2829$ (Sinclair & Duncan, 1972). Berry (1980a) on the other hand, found that this relationship did not hold for Etosha wildebeest, the regression equation for his data being $y = 0{,}90x + 20{,}07$ ($r = 0{,}70$). This represents a considerable difference to other workers' results but he pointed out that Hanks, Cumming, Orpen, Parry & Warren (1976) had suggested that such indices may be over-simplified evaluations of complicated physiological processes which are as yet incompletely understood. However, as this method enables field workers to calculate percentage fat content from dry mass without having to employ the time consuming process of fat extraction in a Soxhlet reflux, it was accepted for the purposes of this study that dry mass of the marrow, corrected for non-fat residue, can give an adequate measure of the fat content of wildebeest marrow samples.

Various workers have described a sequence of fat mobilization as animals lose condition. Riney (1955) gives the sequence as subcutaneous fat being the first to disappear followed by abdominal, perinephric and, finally, bone marrow. This has been confirmed by Sinclair & Duncan (1972) and Brooks *et al*. (1977). This means that bone marrow retains fat until nearly all abdominal and perinephric fat reserves have been depleted and that low BMF values indicate that kidney and other abdominal fat has already been mobilised, while high BMF values may or may not. Thus BMF is inadequate for assessing condition over the full physiological range attainable by ungulates and this places constraints on the interpretation of these data, particularly where BMF levels are high (80%). Furthermore a sequence of mobilisation of BMF from limb bones was described by Brooks *et al.* (1977) in which mobilisation occurs in proximal bones first and is followed by medial and distal bones respectively. This sequence was also described by Reich (1981) from impala in the KNP and Okarma (1984) from red deer (*Cervus elaphus*). These authors are in agreement that for more sensitive comparative studies of condition the femur or humerus should therefore be collected in preference to the metatarsus and metacarpus.

For the purposes of this study, therefore, it was attempted to collect marrow samples from only the femur or humerus and this proved possible in 100% of wildebeest kills (n = 17; 16 femurs, one humerus) found after this aspect of the study was initiated in May, 1983.

Marrow samples were collected from the central portion of the bones to avoid the haemopoietic tissue at the two ends. An ordinary hack saw was used to saw through the bones at two points and after any bone chips had been carefully been removed, the marrow was kept refrigerated in bottles of known mass. Marrow samples were weighed to the nearest 0,01 g and were then dried in an oven at 100°C until constant mass was attained. Dry mass was then expressed as a percentage of the wet mass and the percentage BMF estimated using the equation of Brooks et al. (1977) i.e. % fat = 1,01 X % dry mass - 6,42.

5.2.4 Radio telemetry

In an attempt to gain a deeper insight into the lion/wildebeest relationship, a radio telemetry study of the lion prides in the calving area of Sweni/Mlondozi sub-population was initiated (Figure 5.2.1). This area was selected as it has high densities of wildebeest seasonally (in summer) and relatively few in the winter. Wildebeest in the area in winter tend to be bachelor bulls who stay behind on their territories though some breeding herds also overwinter there. It was thought that seasonal differences in the proportion of wildebeest in the lions' diet could be shown and also a seasonal bias in the sex ratio of kills depending on whether breeding herds were present or absent.

Radio collars were supplied by the National Electrical Engineering Research Institute (N.E.E.R.I.) of the Council for Scientific and Industrial Research (C.S.I.R.) and transmitters (collars) operated at between 150,850 MHz and 151,225 MHz. These collars were supplied as having a battery duration of 2 years and signalled at a pulse rate of 100 pulses per minute. Collars were supplied initially with 70 cm of belting on each side of the transmitter to allow ample overlap and adjustment for both male and female lions. Neck circumferences were found to be in the region of 650 cm for females and 800 cm for males. Belting material used for the collars was 6 cm wide while the transmitter itself, which hung under the neck when fitted, was 9 cm X 8,5 cm X 6 cm (see Plate 5.2.1). Collar mass was around 750 gm.

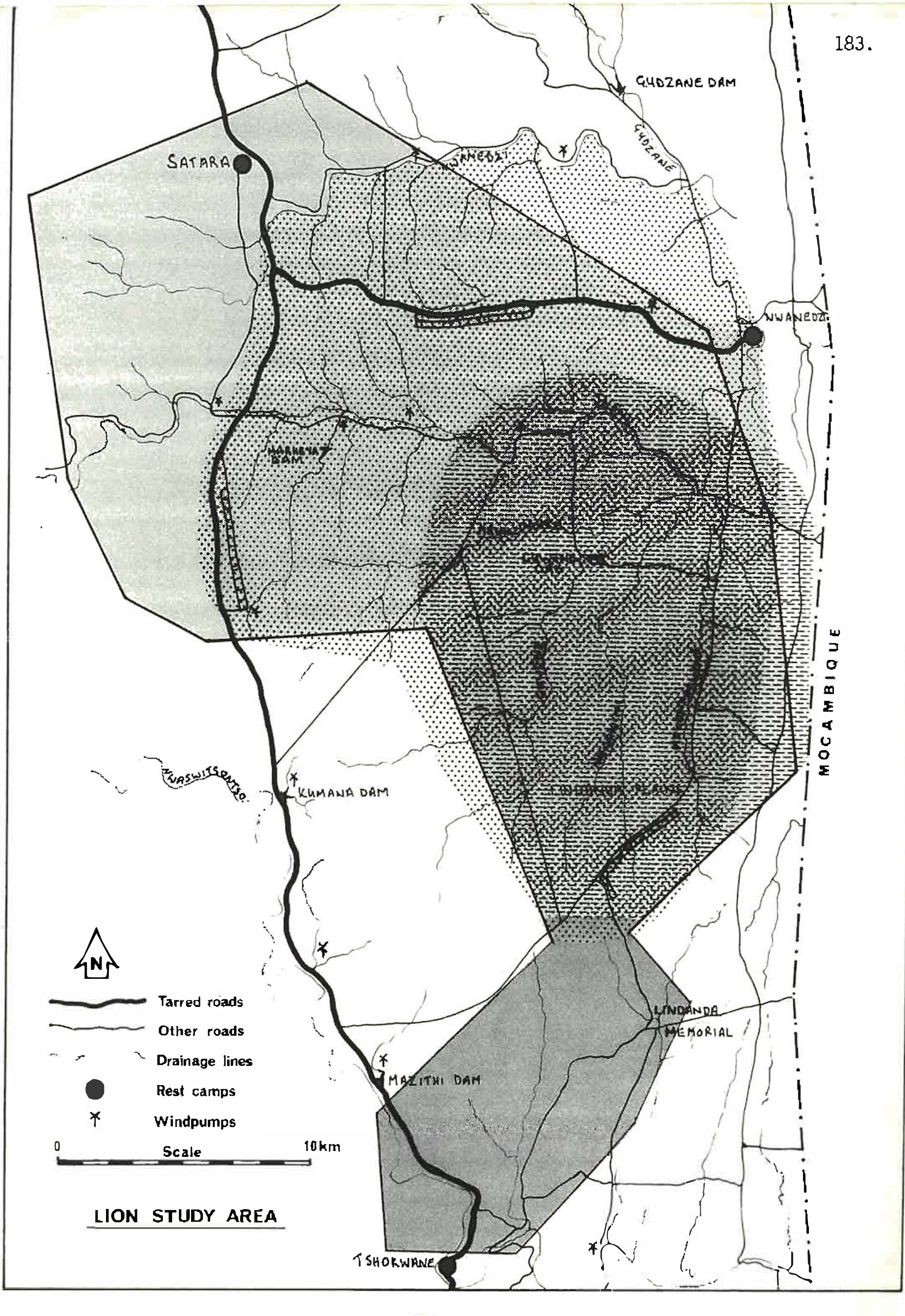
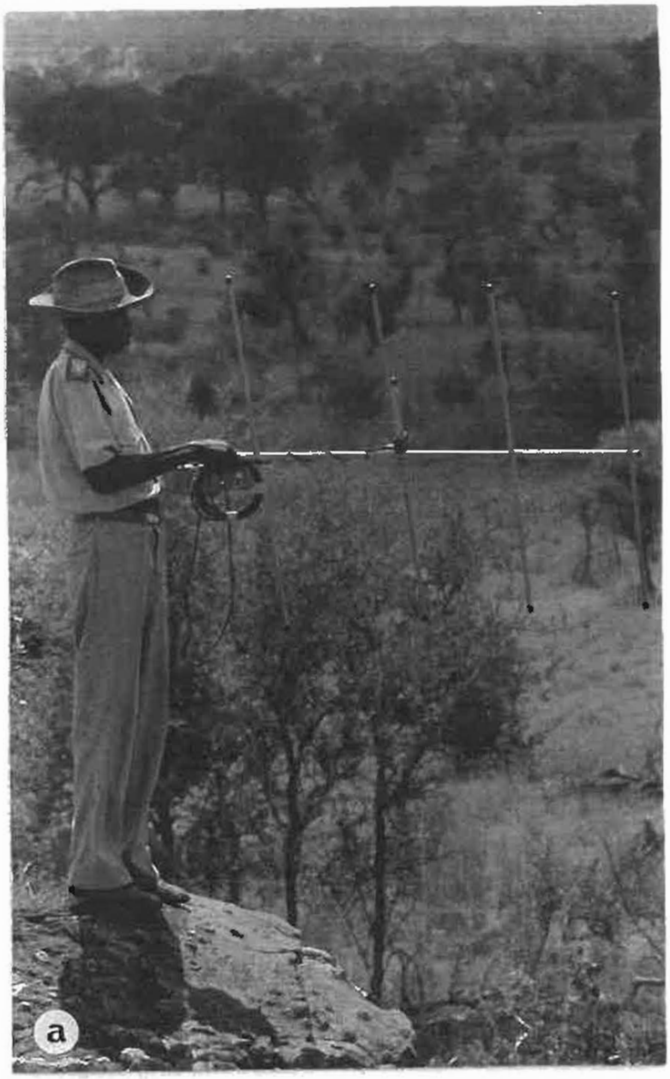
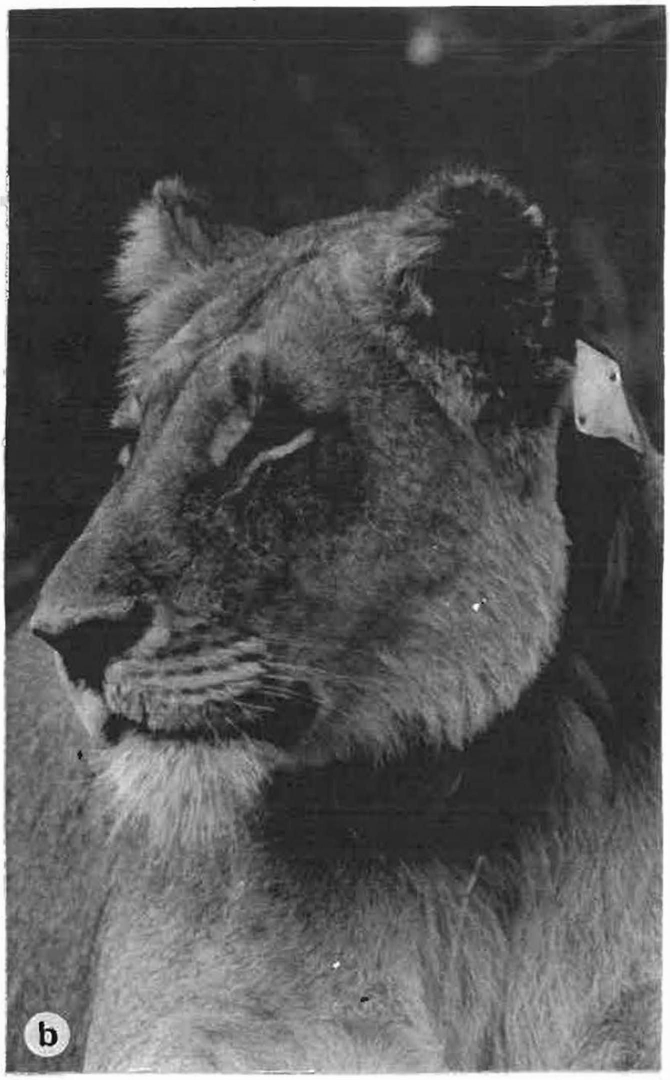


FIGURE 5.2.1: The lion study area ⬭ . This area was also the one in which predator cropping had previously been conducted ⬭ and also where summer aerial surveys were conducted of the wildebeest concentrations in December/January ⬭ .





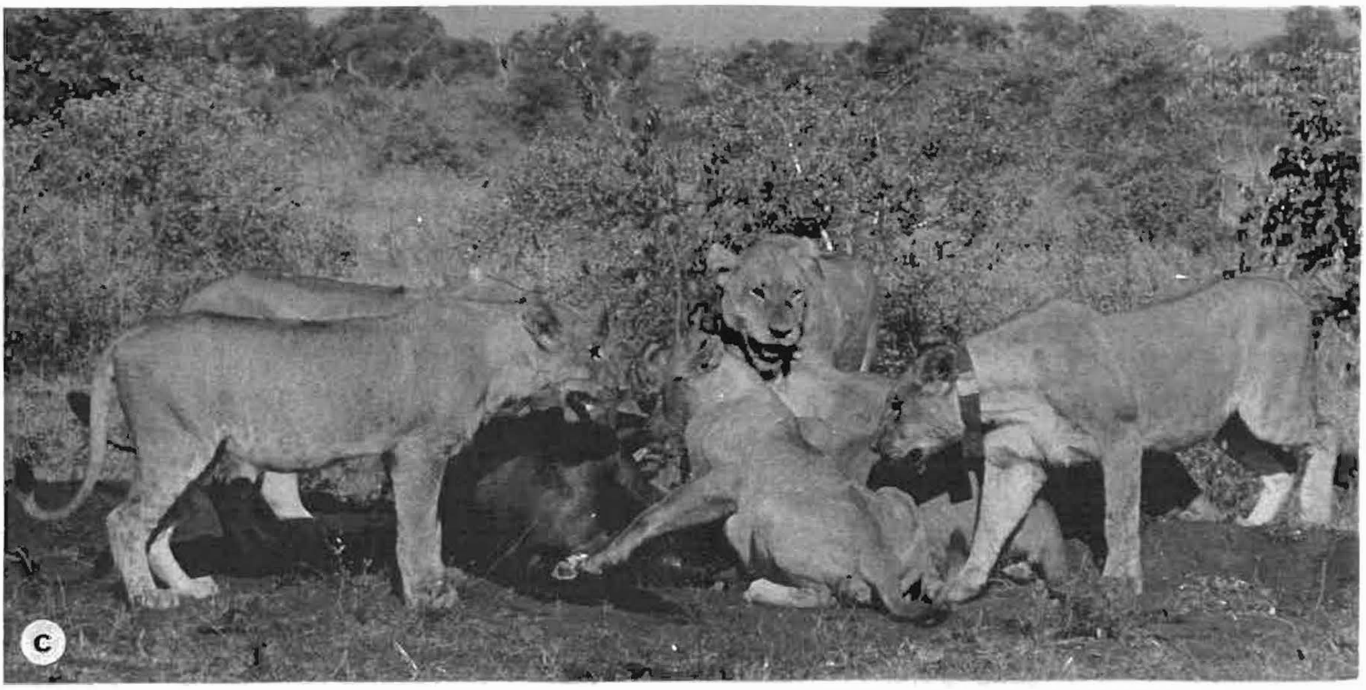


PLATE 5.2.1: (a) The hand held receiver and directional Yagi antenna showing also the use of high ground to obtain initial signals. (b) A collared lioness showing also the position of the transmitter hanging under the neck. (c) A collared lioness and her pride located by means of radio telemetry just after having killed an adult wildebeest bull (note collared female on the right).

Initially lions were caught by the methods of Smuts, Whyte & Dearlove (1977; 1978) which involved attracting the lions to a bait at night by means of scent trails and amplified recorded sounds of lions and hyaenas feeding. The required lions were then selected, immobilised, and fitted with radio collars. Ages were determined according to the method of Smuts, Anderson & Austin (1978). Later on in the study, other lions were fitted with collars on an incidental basis as and when they were encountered in the area. In some cases this also necessitated the use of a bait in order to entice the entire pride out of thick bush to allow a satisfactory selection of the individuals to be collared.

Lions were immobilised using a basic drug cocktail consisting of 200 mg Sernylan (Phencyclidine hydrochloride, Parke-Davis) and 50 mg Rompun (Xylazine hydrochloride, Bayer). This dosage rate of Sernylan conforms to those given by Ebedes (1973) while the Rompun was administered at dosage rates lower than those recommended by Young & Whyte (1973).

Darting equipment was the same as was used for wildebeest capture described in the previous chapter.

Tracking of the marked animals was conducted using a hand-held receiver (Model NNEI Digitaal 224 - also supplied by the C.S.I.R.) and directional Yagi antenna (see Plate 5.2.1).

The procedure for locating collared lions was as follows. An initial signal was obtained from high ground (a small "koppie" or hill).

Having established the direction, the lion was approached by vehicle (4X4 Toyota Hilux), stopping repeatedly for a fresh directional signal until the lion was visually located. Marked lion prides soon became habituated to the vehicle and, if care was taken, they could be approached to within a few metres. Once this had been achieved, the following information could be noted (see Plate 5.2.1).

a) The structure of the group present.
b) Whether they had fed or not.
c) If they had fed, could the prey remains be located.
d) If so, the species, sex and age of the prey.
e) If possible, a bone marrow sample was collected from the prey remains for condition analysis.
f) The precise locality was plotted on a suitable map (1:100 000).
g) Any other pertinent comments.

It was immediately found that the field worker is faced with a basic dilemma when working with more than one pride of lions. Often when having located a pride, it was obvious that they had had a substantial meal and the prey could not be located. Only if the observer had stayed permanently with the pride so as to witness all their kills regardless of whether they were made during day or night would it have been possible to record what the prey item had been. This approach however, limits the scope of the day's/night's work to only one pride and would have meant ignoring the rest of the collared animals for that particular study session. Alternatively, each animal or pride can be tracked each day with the hope that kills that they may have made could still be located. Ideally two teams are needed - one to track all collared animals each day and another to follow a selected pride each night. Shortage of manpower rendered this impossible and thus the majority of work was conducted during daylight and it was attempted to track each pride each day.

As was the case with data from Rangers' returns, analysis of kill data acquired with the assistance of radio telemetry was conducted largely according to the methods of Pienaar (1969b). In this case also, reliable census data from the predator study area (see Figure 5.2.1) were required. Ecological aerial surveys of this area are conducted during the month of June for respective years as part of the annual survey programme (Joubert, 1981; 1982; 1983c; 1984), but due to migratory habits of the zebra and wildebeest of this area, a summer survey, conducted in an identical fashion to the annual surveys (Joubert, 1983b) was also carried out during January in 1982, 1983 and 1984. This was to enable an assessment of seasonal differences in prey potentially available to the lions of this area.

5.2.5 Effect of predator culling

To assess the effect of predator culling, ground counts to monitor the structure of the wildebeest population were initiated in 1978. Between January 1978 and January 1980, lions and hyaenas were culled in the calving area of the Sweni/Mlondozi sub-population. As this was the only sub-population affected by this culling, the Satara sub-population served as a useful control area for comparative purposes. Sub-population trends from ecological aerial survey data (Joubert, 1978-1980) and trends in sub-population structure from ground count data were used to evaluate the effect and success of this predator cropping campaign.

5.3 RESULTS AND DISCUSSION

5.3.1 Rangers' Returns

5.3.1.1 Preference rating of wildebeest in the diet of lions

The first study using the data from Rangers' returns was conducted by Pienaar (1969b). Since the earliest years of the KNP's existence, records have been kept of kills found in the area by organised patrols, but as many of these records had been lost from the archives it was only possible for him to analyse the data for the periods 1933 to 1946 and from 1954 to 1966. For the earlier period of the study, no census data were available and preference ratings could thus not be calculated. This was done for the period 1954 to 1966. Smuts (1975b) continued with the analysis for the subsequent years and completed the picture up to 1975, though the year 1975 was still in progress at the time of writing and the available data for that year were therefore lumped with those of 1974. For the purpose of this study, therefore, data from 1974 and 1975 have been re-analysed as have all the data up to 1983.

For the initial study, Pienaar (1969b) lumped the data for the whole of the 1954 - 1966 period while Smuts (1975b) analysed each year separately in order to detect trends. In this he was partially successful as he could conclude that, "From 1971 onwards there has been a gradual but clear increase in the preference rating for both wildebeest and zebra". Analyses for this study have thus also been conducted on an annual basis. Smuts also only considered the seven major prey species of lions (impala, wildebeest, zebra, buffalo, kudu, waterbuck and giraffe) while Pienaar had included all kills of all species in his analysis. The analysis in this thesis has followed the method of Smuts and included only the above seven species.

Table 5.3.1 gives the analyses of Pienaar (1969b) from 1954 to 1966 (cf. Smuts, 1975b) and of Smuts (1975b) from 1968 to 1974/75 which are included here for the sake of comprehensiveness.

Data extracted from Rangers' returns between 1974 and 1983 are given in Table 5.3.2.

As was found by Smuts (1975b) there is evidence of an increase in the wildebeest preference rating. This increase continued until 1978 when the highest recorded preference rating of 4,05 was obtained. Subsequent to this there was a decline until the end of 1983. This trend is illustrated in Figure 5.3.1

For illustrative purposes, least squares regression lines have been fitted to the data points for the increasing as well as the decreasing phases of this trend (Figure 5.3.1). However, as was the case with cow/calf ratios in the previous chapter, these untransformed ratio data are not suitable for further least squares regression analysis.

Spearman's Rank correlation coefficients indicated a very moderate correlation during the increase phase (r_s = 0,43; $p > 0,1$) but a stronger one for the decreasing phase (r_s = 0,82; p = 0,1). A moderate correlation is not surprising when the nature and sample sizes

Table 5.3.1: Lion kill data (from Rangers' returns) and preference ratings for seven game animals in the Central District of the Kruger National Park between 1954 and 1966 (Pienaar, 1969b) and 1968 and 1974/75 (Smuts, 1975b).

Species	1954/1966			1968			1969			1970		
	No. of kills	Relative freq.(%)	Preference rating	No. of kills	Relative freq.(%)	Preference rating	No. of kills	Relative freq.(%)	Preference rating	No. of kills	Relative freq.(%)	Preference rating
Impala	905	16,0	0,27	61	16,6	0,25	107	22,0	0,34	68	22,2	0,31
Wildebeest	2 162	38,3	2,21	135	36,8	2,70	157	32,3	2,40	68	22,2	2,27
Zebra	942	16,7	1,43	67	18,3	1,54	100	20,6	1,63	46	15,0	1,47
Buffalo	328	5,8	0,91	27	7,4	1,58	39	8,0	1,72	38	12,4	3,01
Kudu	441	7,8	3,46	13	3,5	1,80	14	2,9	1,54	24	7,8	4,00
Waterbuck	513	9,1	4,85	33	9,0	6,11	39	8,0	6,31	24	7,8	7,84
Giraffe	360	6,4	2,69	31	8,4	4,03	30	6,2	2,76	38	12,4	5,71

Species	1971			1972			1973			1974/75		
	No. of kills	Relative freq.(%)	Preference rating	No. of kills	Relative freq.(%)	Preference rating	No. of kills	Relative freq.(%)	Preference rating	No. of kills	Relative freq.(%)	Preference rating
Impala	80	23,9	0,33	107	31,6	0,43	87	23,9	0,33	110	27,9	0,39
Wildebeest	94	28,1	2,94	75	22,1	2,86	88	24,2	3,08	119	30,2	4,35
Zebra	61	18,3	2,19	63	18,6	2,07	76	20,9	2,37	62	15,7	2,03
Buffalo	32	9,6	1,86	34	10,0	1,86	34	9,3	1,57	36	9,1	1,33
Kudu	12	3,6	2,00	12	3,5	1,64	22	6,0	2,42	20	5,1	2,01
Waterbuck	27	8,1	10,22	18	5,3	5,63	27	7,4	6,86	17	4,3	3,92
Giraffe	28	8,4	3,74	30	8,8	3,59	30	8,2	3,12	30	7,6	2,84

Table 5.3.2: Lion kill data analyses for seven large prey species from the Central District between 1974 and 1983. (Data extracted from Rangers' returns).

Year	Parameter	Impala	Wilde-beest	Zebra	Buffalo	Kudu	Water-buck	Giraffe	Total
1974	No.kills[1]	56	75	23	15	4	5	12	190
	Rel.freq[2]	29,5	39,5	12,1	7,9	2,1	2,6	6,3	-
	Census[3]	38200**	7223*	8650	6772	1243*	1070	2304*	65462
	Rel.freq[4]	58,4	11,0	13,2	10,3	1,9	1,6	3,5	-
	Pref.rat[5]	0,51	3,59	0,92	0,77	1,11	1,63	1,80	-
1975	No. kills	54	44	39	21	16	12	18	204
	Rel.freq.	26,5	21,6	19,1	10,3	7,8	5,9	8,8	-
	Census	38200**	6745	7523	6597	1382	988***	2007	63442
	Rel.freq.	60,2	10,6	11,9	10,4	2,2	1,6	3,2	-
	Pref.rat.	0,44	2,04	1,61	0,99	3,55	3,69	2,75	-
1976	No. kills	42	40	39	9	19	9	20	178
	Rel.freq.	23,6	22,5	21,9	5,1	10,7	5,1	11,2	-
	Census	30937	5783	7616	7655	1583	905	2213	56692
	Rel.freq.	54,6	10,2	13,4	13,5	2,8	1,6	3,9	-
	Pref.rat.	0,43	2,20	1,63	0,38	3,82	3,19	2,87	-
1977	No. kills	23	47	36	13	8	5	21	153
	Rel.freq.	15,0	30,7	23,5	8,5	5,2	3,3	13,7	-
	Census	28326	4569	7649	8747	2126	735	2124	54276
	Rel.freq.	52,2	8,4	14,1	16,1	3,9	1,4	3,9	-
	Pref.rat.	0,29	3,65	1,67	0,53	1,33	2,41	3,51	-
1978	No. kills	18	46	27	12	6	6	22	137
	Rel.freq.	13,1	33,6	19,7	8,8	4,4	4,4	16,1	-
	Census	33034	5141	8316	8430	3362	1026	2764	62073
	Rel.freq.	53,2	8,3	13,4	13,6	5,4	1,7	4,5	-
	Pref.rat	0,23	4,05	1,47	0,65	0,81	2,59	3,58	-
1979	No. kills	17	31	24	5	33	9	32	151
	Rel.freq.	11,3	20,5	15,9	3,3	21,9	6,0	21,2	-
	Census	35340	4768	8434	8491	3488	1008	2834	64363
	Rel.freq.	54,9	7,4	13,1	13,2	5,4	1,6	4,4	-
	Pref.rat.	0,21	2,77	1,21	0,25	4,06	3,75	4,82	-
1980	No. kills	13	34	25	23	25	9	19	148
	Rel.freq.	8,8	23,0	16,9	15,5	16,9	6,1	12,8	-
	Census	38288	5816	8877	8551	3060	1039	2641	68272
	Rel.freq.	56,1	8,5	13,0	12,5	4,5	1,5	3,9	-
	Pref.rat.	0,16	2,70	1,30	1,24	3,77	4,00	3,32	-
1981	No. kills	17	31	23	16	17	5	17	126
	Rel.freq.	13,5	24,6	18,3	12,7	13,5	4,0	13,5	-
	Census	49655	6512	10834	11214	3956	1506	3146	86823
	Rel.freq.	57,2	7,5	12,5	12,9	4,6	1,7	3,6	-
	Pref.rat.	0,24	3,28	1,46	0,98	2,96	2,29	3,72	-

(Table 5.3.2. continued overleaf)

Table 5.3.2 (continued)

Year	Parameter	Impala	Wilde-beest	Zebra	Buffalo	Kudu	Water-buck	Giraffe	Total
1982	No. kills Rel.freq. Census Rel.freq. Pref.rat.	20 15,2 54425 57,6 0,26	20 15,2 8127 8,6 1,76	16 12,1 11603 12,3 0,99	35 26,5 11481 12,1 2,18	23 17,4 4113 4,4 4,00	5 3,8 1486 1,6 2,36	13 9,8 3288 3,5 2,83	132 94523
1983	No. kills Rel.freq. Census Rel.freq. Pref.rat.	18 11,9 35508 53,1 0,22	24 15,9 7584 11,3 1,40	10 6,6 9807 14,7 0,45	62 41,1 7584 11,3 3,62	8 5,3 2468 3,7 1,44	12 7,9 1044 1,6 5,09	17 11,3 2869 4,3 2,62	151 66864
1974 to 1983	No. kills Rel.freq. Census Rel.freq. Pref.rat.	280 17,8 381913 55,9 0,32	392 25,0 62268 9,1 2,74	262 16,7 89309 13,1 1,28	211 13,4 85522 12,5 1,07	159 10,1 26781 3,9 2,58	75 4,8 10807 1,6 3,02	191 12,2 26190 3,8 3,17	1570 682790

1. Number of kills per species recorded per year.
2. Relative frequency (%) of each species in the kill sample.
3. Census totals for each species from the Central District per year.
4. Relative frequency (%) of each species in the census total.
5. Preference rating. (See text for calculation procedure).

* Average of 1975 and 1973 counts
** Average of totals from 1976 to 1983 censuses rounded to the nearest 100.
*** Average of 1974 and 1976 counts.

of the data are considered. However, there are only two data points (1975 and 1976) which do not conform with the increasing trend between 1966 and 1978, but these affect the correlation accordingly. These two points fall in a slightly drier period of the wet cycle which suggest that conditions may have rendered wildebeest less vulnerable to lions at that time, but the continuing decline in the population over the same period does not support this.

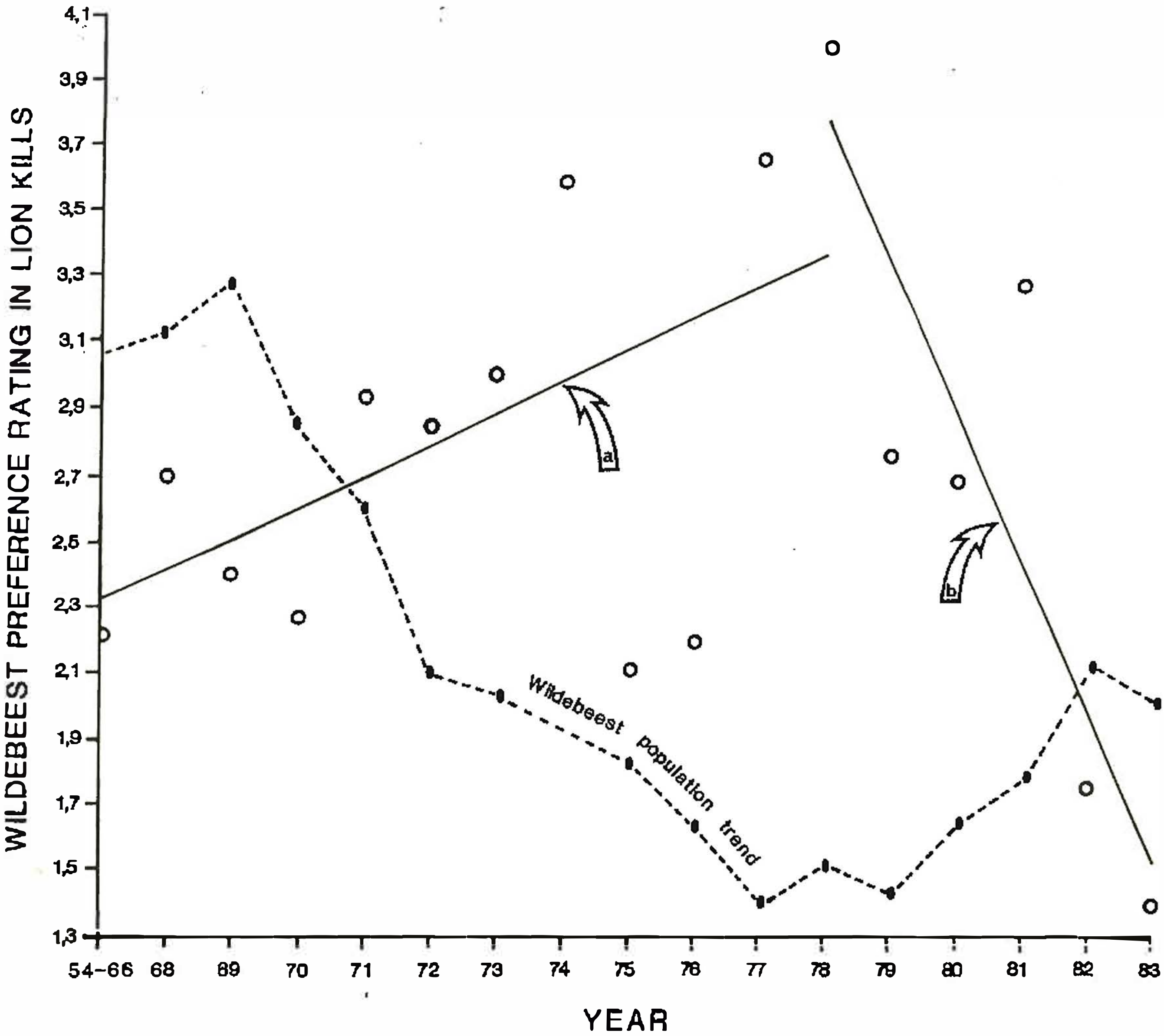


FIGURE 5.3.1: Annual preference ratings of wildebeest in the diet of lions in the Central District of the Kruger National Park between 1954-1966 and 1983. Least squares regression lines fitted to the data points indicate the trends: (a) the increasing phase between 1946 and 1978 and (b) the declining phase between 1978 and 1983. See text for further explanation.

Another factor which may affect these preference ratings is that the period included for each year's calculations runs from January to December and thus encompasses parts of two summers or rainy seasons. An analysis of the data for the months July to the following June, and which thus considered each rainy season individually may have given closer correlations and therefore indicated the trend more clearly. Smuts (1975b) however, used the period January to December, and this analysis conformed to his method to make comparisons possible.

It can be seen from Figure 5.3.1 that the trend in the wildebeest preference ratings roughly followed the reverse image of the population trend. This is according to expectation because if the predation pressure remains high on a declining population, the relative proportion of that species in the kill sample would remain high while the actual proportion of that species in the prey community would decrease thus giving higher and higher preference ratings. Conversely, when the predation pressure is relieved (for whatever reason) the proportion of that species will decline in the kill sample, and the increasing population will lower the preference rating. Thus it would seem that the preference rating can provide a valuable measure of a prey population's vulnerability to a predator under any particular set of prevailing environmental conditions.

There was also a declining trend in the number of wildebeest found killed by lions from 1968 to 1983 (see Tables 5.3.1 and 5.3.2). The highest recorded number of kills was 157 in 1969 while the lowest was 20 in 1982. Fig. 5.3.2 illustrates the data and shows that the decline was curvilinear. For illustrative purposes respective parabolic curves were fitted to these data as well as to the wildebeest

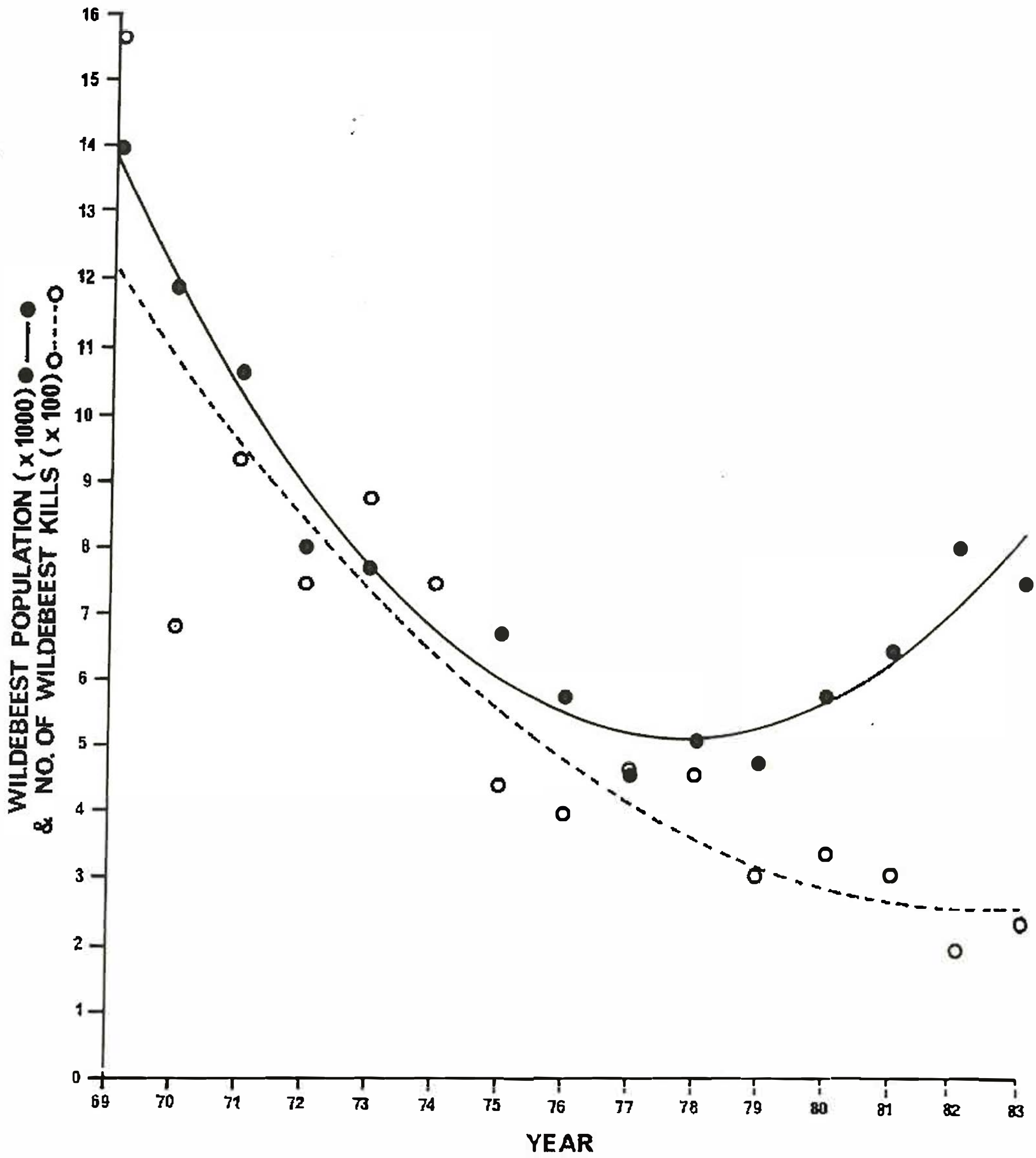


FIGURE 5.3.2: Parabolic curves fitted to the annual census totals of the wildebeest population of the Central District and also to the total number of wildebeest found killed by lions in the area per year between 1969 and 1983. (See text for further explanation).

population data. These curves could be described by the equations $y = 153{,}915 - 16{,}6335x + 0{,}542338x^2$ ($r^2 = 0{,}798$; F-test = 23,67; $p < 0{,}01$ (Sokal & Rohlf, 1969)) and $y = 18226{,}5 - 2439{,}98x + 113{,}649x^2$ ($r^2 = 0{,}963$; F-test = 144,28; $p < 0{,}01$).

This decrease in the number of kills per year was also to be expected. As the population decreased, less individuals were available to the lions as potential prey while after the nadir, the reduced predation rate allowed for the population increase. Speculation on possible future trends suggests that the predation rate (number of kills) will increase as and when further population increases occur, and that future cyclical increases and decreases in the wildebeest population will be tracked by increases and decreases in the number of wildebeest killed by lions.

This cycle is similar to those described for lynx (Lynx lynx) and snowshoe hare (Lepus americanus) populations (Bergerud, 1983) but whereas, in the cycles described here it is the number of kills which "tracks" the wildebeest population cycle, it is the lynx population which tracks the snowshoe hare population in that situation. The wolf (Canis lupus) population of Isle Royale has also been reported to track the population cycles of its prey the moose (Alces alces) (Mech, 1966; Peterson & Page, 1983; Peterson, Page & Dodge, 1984). Lions, however, have a far greater diversity in alternative prey species than do lynx and wolves in simpler ecosystems and thus can switch to other prey species allowing a greater population stability than predators who are more specifically dependent on a single prey species.

Evidence for a shift in vulnerability from wildebeest to waterbuck is given by the data in Table 5.3.2. Any trend in the preference rating of wildebeest from one year to the next (either positive or negative) was in every case but one (1977-1978) marked by a concomitant opposite trend in the preference rating of waterbuck. The preference ratings, when plotted against each other, also indicate this inverse relationship - when wildebeest preference ratings are high, those of waterbuck tend to be low and vice versa (Figure 5.3.3). A least squares regression line has been fitted to the data points which can be described by the equation $y = 5,19 - 0,76x$. This relationship gave only a very modest correlation (Spearman's Rank $r_s = 0,491$; $p > 0,1$). This means that the switch by lions from one of the prey species to the other may not necessarily be proportionate (probably due to the wide number of other species in the lions' potential prey spectrum), but the consistency of the inverse trends of the two species' preference ratios from year to year indicate that such a switch does in fact occur. This seems reasonable when it is considered that these two species are the only two medium sized grazers in the prey spectrum considered in this sample and in the KNP they probably represent ecological counterparts - the wildebeest being a short grass grazer and the waterbuck prefering longer grass conditions. A change in habitat towards longer grass conditions would thus tend to favour waterbuck and the predation rate on wildebeest by lions would probably increase while in shorter grass conditions the reverse would probably hold true.

5.3.1.2 Sex, age and seasonal analyses of wildebeest killed by lions

Pienaar (1969b) tabulated the sexes and ages of wildebeest killed by lions in the KNP betwen 1966 and 1968 and are given in Table 5.3.3 to facilitate comparison.

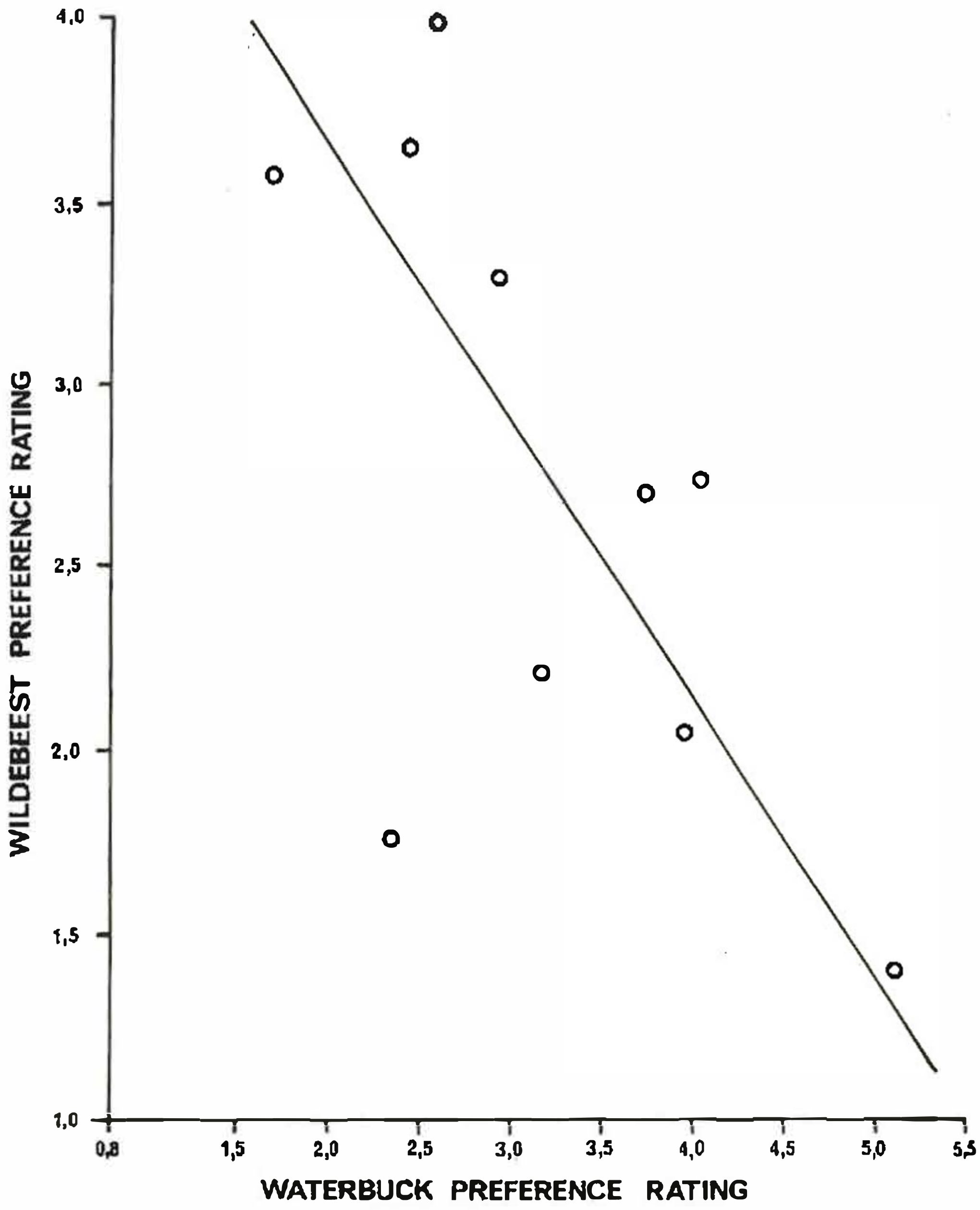


FIGURE 5.3.3: The inverse relationship between preference ratings of wildebeest and waterbuck in the diet of lions in the Central District of the Kruger National Park.

Table 5.3.3: Analyses of carcass data of wildebeest killed by lions in the Kruger National Park according to sex, age and time of year (February 1966 to January 1966).

Age/ sex class	Feb.-Apr.*		May-July**		Aug.-Oct.**		Nov.-Jan*		Total	
	n	%	n	%	n	%	n	%	n	%
Adult	91	73,39	105	64,82	125	72,26	106	75,17	427	71,18
Yearl.	12	9,68	13	8,02	15	8,67	14	9,93	54	9,00
Calves	7	5,64	5	3,09	9	5,20	8	5,68	29	4,82
Indet.	14	11,29	39	24,07	24	13,87	13	9,22	90	15,00
TOTAL	124	100,00	162	100,00	173	100,00	141	100,00	600	100,00
Bulls	70	56,45	77	47,53	82	47,40	59	41,85	288	48,00
Cows	40	32,26	46	28,40	67	38,73	65	46,09	218	36,34
Indet.	14	11,29	39	24,07	24	13,87	17	12,06	94	15,66
TOTAL	124	100,00	162	100,00	173	100,00	141	100,00	600	100,00

* Summer
** Winter

Although these data were derived from only a two year period, they are comparable to those of the later period (1975 to 1983) given in Table 5.3.4.

From the data in these two tables, various aspects of interest emerge:

a) Sex Ratio. A significent difference was found in the sex ratio of the wildebeest killed by lions during both periods. Pienaar had a sex ratio of 288 bulls to 218 cows in his sample (χ^2 = 9,68; $p<0,005$) while between 1975 and 1983 there were 156 bulls to 111 cows (χ^2 = 7,58; $p<0,01$). Separate analyses of the summer and winter data however, showed that in summer no difference from parity was recorded (Pienaar - 129 bulls to 105 cows (χ^2 = 2,49; $p>0,1$); this study - 70 bulls to 59 cows (χ^2 = 0,94; $p>0,1$)).

Table 5.3.4: Age and sex data of wildebeest killed by lions in the Central District of the Kruger National Park according to sex and age and the time of year killed (summer or winter). Data extracted from Rangers' returns.

YEAR	SUMMER												WINTER											
	Ad.			Sub-Ad.			Calf			Total			Ad.			Sub.Ad.			Calf			Total		
	M*	F	U	M	F	U	M	F	U	M	F	U	M	F	U	M	F	U	M	F	U	M	F	U
75	11	9	2	1	-	1	2	-	-	14	9	3	11	5	-	-	-	-	1	-	-	12	5	-
76	8	6	1	-	-	1	-	-	1	8	6	3	14	4	1	1	-	2	-	-	1	15	4	4
77	11	6	1	-	-	-	1	-	6	12	6	7	9	8	2	-	1	-	-	-	2	9	11	4
78	9	7	2	2	1	-	-	-	1	11	8	3	9	9	-	1	2	2	1	-	-	11	9	2
79**	7	8	1	1	1	-	-	-	-	8	9	1	5	3	2	-	-	1	-	-	-	5	3	3
80**	10	9	1	-	-	-	-	-	1	10	9	2	6	5	1	1	-	-	-	-	-	7	5	1
81**	7	7	1	-	-	1	-	-	-	7	7	2	6	4	3	-	-	1	-	-	1	6	4	5
82**	3	4	2	-	1	-	-	-	1	3	5	3	7	2	1	-	-	-	-	-	-	7	2	1
83	4	3	1	-	-	-	-	-	-	4	3	1	7	6	-	-	-	-	-	-	-	7	6	-
TOT.	70	59	12	4	3	3	3	-	10	77	62	25	74	46	10	3	3	6	2	-	4	79	49	20

* M = male; F = female; U = sex uncertain.
** The period of the decline in the proportion of cows to bulls in the wildebeest population (see Chapter 4).

This did not hold for winter data (Pienaar - 159 bulls to 113 cows (χ^2 = 7,78; $p<0,01$); this study - 74 bulls to 46 cows (χ^2 = 6,53; $p<0,025$)).

This means that in summer, bulls and cows are taken by lions at a 1:1 ratio while during the winter there is either an increase in the number of bulls killed or a decrease in the number of cows killed by lions. Reasons for this switch are not clear, but it is of interest that whichever of the above two possibilities may be correct, it is in contrast to the cow/calf ratio data given in Chapter 4 (see Figure 4.3.14 and its related text) which suggest that there is an increase in cow mortality in winter (July to October). The available data are inadequate to resolve these conflicting inferences however and more specific attention to this aspect is required.

No significant difference could be found to exist in the sex ratio of the subsample of the data from the years 1979 to 1982 and the rest of the sample. This is the period during which the decline in the proportion of adult cows to bulls occurred. Thus, in spite of the declining proportion of cows in the population, there was no concomitant increase in the recorded number of cows killed by lions. This lends support to the possibility that it was not an increase in cow mortality which skewed the adult sex ratio but that it was caused by one or more calf cohorts with initially skewed sex ratios entering the adult segment of the population (see sub-section 4.4.4.1).

b) Sex and age structure of the two kill samples. No significant differences could be found to exist between the age and sex structure of Pienaar's sample and that of this study. Yearlings and calves were recorded in the same proportion to adults in both samples and the sex ratios of the two samples did not differ ($p > 0,1$ in all cases). This suggests that although there occurred fluctuations of both population size and structure during the sampling periods, sex and age classes of wildebeest killed by lions did not and they are thus taken at similar proportions by lions regardless of population size and structure.

5.3.2 Found wildebeest skulls

Wildebeest in the CD of the KNP are born at or close to a sex ratio of 1:1. Braack (1973) recorded a sample of 50 males to 71 females ($\chi^2 = 3,64$; $p > 0,05$) between 1967 and 1972. In the adult segment of the population however, the sex ratio is distorted in favour of the females. From the total of 20 377 adult wildebeest (older than 2 years) sexed during ground counts between January 1978 and January 1984, 6 751 were bulls and 13 626 were cows. This gives a mean ratio of 1 bull to 2,02 cows (χ^2 = 2 319,6; $p<0,001$).

If a species has a natal sex ratio of 1:1, they must also ultimately die at that ratio (i.e. if the skulls of all individuals of that species that had died could be located, the sex ratio of the skull sample would be 1 male to 1 female). However, if in that species live adults occur at a sex ratio other than parity, age-differential mortality must have occurred. In the wildebeest population of the CD therefore, it is obvious that a greater mortality rate is experienced by the male segment at a younger age than the female segment. This is corroborated by the respective male and female age distributions from the found skull sample. Of the 246 skulls found, 173 could be aged according to the method of Attwell (1980). This sex and age distribution is given in Table 5.3.5 and illustrated in Figure 5.3.4.

Two things are apparent from Table 5.3.5 and Figure 5.3.4. The first is that a greater proportion of bull skulls in the younger age classes (< 9-10yr age class) were found while there were more cows in the older age classes. Chi-squared tests (contingency table) on animals older (21 bulls to 28 cows) against those younger (89 bulls to 35 cows) than nine years respectively also showed a significant difference (χ^2 = 11,46; $p<0,001$).

This means that bulls were in fact being killed in greater proportions at a younger age than cows. The critical age for both bulls and cows would appear to be around six to eight years. A large

Table 5.3.5: The age and sex structure of a found sample of 173 wildebeest skulls in the Central District of the Kruger National Park.

Age class (yrs)	Bulls		Cows		Total	
	No.	Frequency (%)	No.	Frequency (%)	No.	Frequency (%)
18-21	-	0,00	-	0,00	-	0,00
15-18	-	0,00	1	0,58	1	0,58
14-15	1	0,58	1	0,58	2	1,16
13-14	4	2,31	7	4,05	11	6,36
12-13	2	1,16	7	4,05	9	5,20
11-12	4	2,31	3	1,73	7	4,05
10-11	3	1,73	3	1,73	6	3,47
9-10	6	3,47	6	3,47	12	6,94
8-9	12	6,94	6	3,47	18	10,40
7-8	19	10,98	7	4,05	26	15,03
6-7	20	11,56	7	4,05	27	15,61
5-6	12	6,94	6	3,47	18	10,40
4-5	14	8,09	3	1,73	17	9,83
3-4	10	5,78	2	1,16	12	6,94
2-3	1	0,58	3	1,73	4	2,31
1-2	2	1,16	1	0,58	3	1,73
0-1	-	0,00	-	0,00	-	0,00
Total	110	63,60	63	36,40	173	100,01

proportion of the bulls had been killed before they were eight years old while if a cow survived to eight years, it seems that she would have a good chance of attaining old age, as a high proportion of the cows in the sample survived to the 12-14 year old age class. The high proportion of 12-14 year olds is however, not indicative of a stationary age distribution.

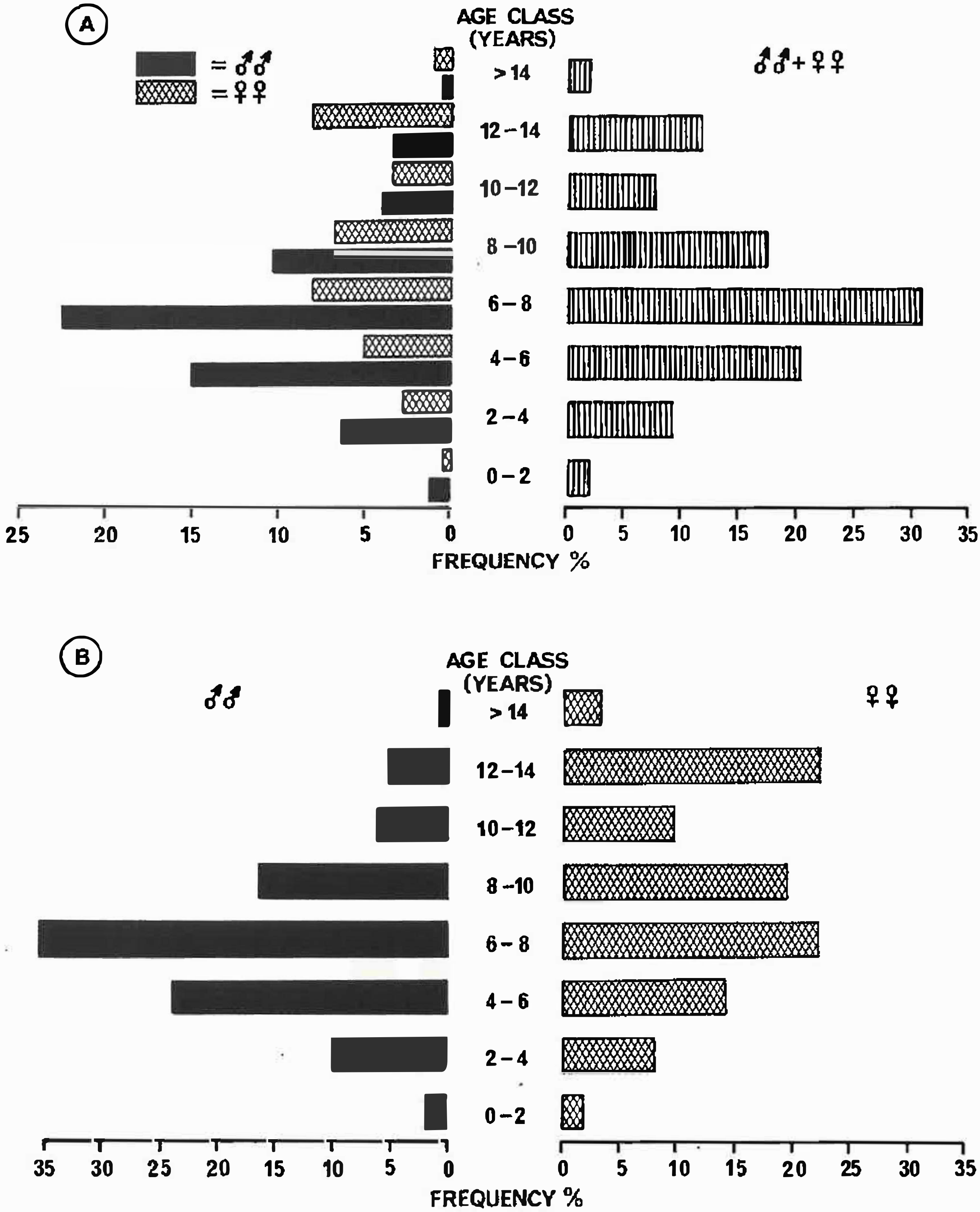


FIGURE 5.3.4: Age and sex frequency distribution at death of 173 found wildebeest skulls in the Central District of the Kruger National Park. (A) shows the distribution of bulls and cows on the left of the axis and bulls plus cows on the right. (B) shows the distribution of bulls (left) and cows (right) treated as independent samples.

Some authors (e.g. for waterbuck (Melton, 1983)) have used found skull samples to construct life tables for the calculation of r_s. This type of analysis probably has closer affinities to those in the previous chapter, but as the skull sample has been considered for the purposes of this study from a predation point of view, such analyses may have provided a useful insight into the impact of lion predation and they are therefore discussed here in the predator-prey section.

Caughley (1977) defines r_s as the demographic vigour (survival-fecundity rate of increase) of the population as it weighs up and combines the vigour of each sex and age class in the sampled population. However, the method requires as a pre-requisite that the population should have a stationary age structure.

The histograms in Figure 5.3.4 suggest that there is a stationary age structure in the bull segment of the population though the skewing of the sex ratio (see Chapter 4) does not support this. The sexes of this sample could not be combined for life table purposes, however, as it was shown that the age distribution of the two sexes were significantly different (Kolmogorov-Smirnov two sample test: $D = 0,26$; $p < 0,01$ (two tailed)). Data from the female segment of this skull sample also showed significantly different distributions when separated into older (longer since death) and newer (fresher) subsamples.

Table 5.3.6 gives these two distributions. Skulls from age (age since death) classes 1-6 were assigned to one category (fresher skulls) while all the rest were assigned to the other (see Methods for age classes).

Table 5.3.6: Age (since birth) distribution of skulls of wildebeest cows assigned to two categories (fresh and decayed) of age since death for the purposes of testing for stable age distribution over time (Kolmogorov-Smirnov test).

Age of cow since birth	Fresh skulls			Decayed skulls			(A)-(B) D max
	No.	Cum.Freq.	Rel. Cum. Freq. (A)	No.	Cum.Freq.	Rel. Cum. Freq. (B)	
1	1	1	0,022	-	0	0,000	
2	3	4	0,089	-	0	0,000	
3	2	6	0,133	-	0	0,000	
4	3	9	0,200	-	0	0,000	
5	5	14	0,311	1	1	0,056	
6	6	20	0,444	-	1	0,056	0,388
7	4	24	0,533	4	5	0,278	
8	2	26	0,577	4	9	0,500	
9	4	30	0,667	2	11	0,611	
10	2	32	0,711	1	12	0,667	
11	3	35	0,778	-	12	0,667	
12	6	41	0,911	1	13	0,722	
13	3	44	0,978	4	17	0,944	
14	-	44	0,978	1	18	1,000	
15-18	1	45	1,000	-	18	1,000	
>18	-	45	1,000	-	18	1,000	
Total	45			18			

The two age distributions were therefore found to be significantly different ($D = 0,388$; $p < 0,05$ (two tailed)) which indicates that the age distribution of the population has changed over time and thus the use of a life table for the calculation of r_s is invalid. The calculation of r_s from these data would also be spurious when reliable census data are available for the accurate calculation of $\bar{r}$.

The assignment of skulls to classes according to the degree of decay also enabled an assessment of change in sex specific mortality over time. Such change could corroborate the possibility that it was increased female mortality which contributed to the skewing of the adult sex ratio (see Chapter 4).

Although only some of the skulls (n = 173) could have age at death estimated depending on the presence or absence of suitable teeth, all of the skulls were sexed (n = 246). All of these could also be assigned to a class indicating the degree of decay, and due to the relatively small sample size, these were lumped into three classes for the analysis.

Table 5.3.7: Sex ratios of wildebeest skulls at various stages of decay.

Stage of decay	Bulls	Cows	Sex ratio (cows/bull)
A*	43	26	0,605
B**	31	23	0,742
C***	78	45	0,577
Total	152	94	0,618

* A = decay classes 1, 2 & 3 (See methods for these classes)

** B = decay classes 4, 5 & 6

*** C = decay classes 7 & 8.

In a contingency table test these data showed no significant differences (χ^2 = 0,60; df = 2; $p > 0,5$) and according to the found skull sample there was no evidence of a change in sex specific mortality rates over time. This lends further support to the possibility that it was not differential mortality favouring bulls which led to a decline in the sex ratio (cows per bull).

5.3.3. Condition of wildebeest killed by lions

It is known that certain predators will "test" prey herds for individuals which may be sick or injured. This testing is effected by putting potential prey herds to flight - a process which enables them to identify and select physically inferior animals which may be more easily overpowered. This method, however, is utilized mainly by the more cursorial species like wild dog (Reich, 1981; Schaller, 1972), hyaena (Kruuk, 1972) and the wolf (Canis lupus) (Mech, 1966) while the ability of lions (who hunt more by stealth) to identify and utilize physically inferior prey individuals is either unknown or does not exist. Varying conclusions have been drawn by various investigators. Schaller (1972) concluded that Serengeti lions predominantly kill wildebeest in good health. Elliot and McTaggart Cowan (1978) found that lions in the Ngorongoro Crater did not rely on young, old or debilitated prey although they "disproportionately captured these types through increased success in most phases of prey capture", and Mills (1984) concluded that in the Kalahari, lions were the most important predators of adult wildebeest and that they tended to remove mainly older animals. None of these studies, however, have concentrated more specifically on the physical condition of wildebeest killed by these predators.

In spite of the lack of published data, it seems likely that although lions do not test prey herds for physically inferior individuals, these animals may still make up a significant proportion of the lions diet. The lion's hunting strategy relies mainly on stealth and a certain degree of co-operation among pride members, and although it is certain that prey animals in prime condition may be captured by these means, it is likely that animals in poorer condition will be more vulnerable to attacks by lions due to reduced vigilance or slower reaction times.

Physical condition may therefore inherently represent the degree to which an individual of a prey species is vulnerable to its predators.

The collection of bone marrow samples from carcasses of animals killed by lions was initiated rather late in the study (May 1983) and this resulted in the relatively small sample from wildebeest (n = 17). Pertinent data are given in Table 5.3.8.

Table 5.3.8: Estimated % bone marrow fat (BMF) of wildebeest killed by lions in the Central District of the Kruger National Park. Date of collection and sex and age of the wildebeest are also given.

Date	Season	Sex	Age*	Marrow sample source	Sample wet wt. (gms)	Sample dry wt. (gms)	Dry wt.% of wet wt.	Estimated BMF**
17-05-83	Dry	M	13	Femur	27,44	14,57	53,10	47,2
08-06-83	"	M	7	"	26,58	2,97	11,17	4,9
14-07-83	"	F	8	"	64,10	61,70	96,26	90,8
02-04-84	"	F	9	"	14,21	8,32	58,50	52,7
02-04-84	"	M	6	"	18,84	4,50	23,89	17,7
07-04-84	"	F	7	"	12,41	11,63	93,71	88,2
12-04-84	"	M	7	"	14,67	11,42	77,85	77,2
12-06-84	"	M	13	"	28,22	2,65	9,39	3,1
22-06-84	"	M	8	"	24,28	8,90	36,66	30,6
25-06-84	"	F	11	Humerus	18,08	9,34	51,66	45,8
27-06-84	"	M	7	Femur	16,92	14,90	88,06	82,5
10-07-84	"	M	10	"	22,17	4,90	22,15	16,0
05-09-83	Wet	M	6	"	18,30	14,88	81,31	75,7
30-09-83	"	M	3	"	25,19	23,37	92,77	87,2
31-03-84	"	M	6	"	19,50	18,00	92,50	87,0
02-11-83	"	M	10	"	16,63	13,18	79,25	73,6
30-03-84	"	M	11	"	29,68	25,67	86,50	80,9

* Ages (in years) determined after the method of Attwell (1980).

** Determined after the equation: % fat = 1,01 X % dry wt.-6,42 (Brooks <u>et al.</u>, 1977).

This sample is unfortunately too small to enable any meaningful interpretation. The wide variation in dry season BMF's rendered a large standard deviation and thus no significant difference could be obtained between wet and dry season results (dry season mean = 46,4; SD = 32,48. Wet season mean = 80,1; S.D. = 6,27. Mann-Whitney U = 15,0; p>0,1). A sub-sample of bulls killed during wet and dry seasons respectively did however produce a significant difference (wet season mean = 46,4; S.D. = 32,4. Dry season mean = 34,9; S.D. = 31,1. Mann-Whitney U = 5,0; p = 0,001). All this says, however, is that wildebeest bulls killed by lions in winter were in poorer condition than those killed in summer, but it does not infer that wildebeest killed by lions were in poorer condition than those others in the population who had escaped these predators.

No published data are available from a shot sample to enable such a comparison. Attwell (1978) did not publish his raw data from wildebeest in Zululand and Berry (1980a), although publishing his data, found that BMF analyses of wildebeest in Etosha did not conform to the pattern of those in other published reports. This renders comparison with similar data from Etosha wildebeest a dubious procedure until the matter is clarified.

The only data as yet available for the KNP are from a sample of six wildebeest bulls shot during late winter. For comparative purposes these data have been supplied by Mills (pers. comm.), but here also the sample is too small to enable a significant analysis. The range of his small sample appears to conform largely to that in this sample (n = 6; mean = 25,8; S.D. = 32,6). Mills' data, when tested against those of bulls killed by lions in winter showed no significant difference (Mann-Whitney U = 20; p = 0,331).

MILLS, M.G.M. Private Bag X402, Skukuza, 1350. Kruger National Park, South Africa.

5.3.4 Radio telemetry

A total of 15 different lions were fitted with radio collars during the study period, which enabled contact at various times and for various lengths of time with 10 prides or groups (use of the word pride refers to the pride as a whole, while "group" refers to sub-groups of the pride). Apart from the quarterly ground counts of wildebeest, the tracking of these collared lions and their prides occupied the majority of time spent doing field work. Results of this study will be published elsewhere (Whyte, in prep. a) with the exception of the information related to predator-prey relationships with wildebeest which is presented here.

5.3.4.1 The lions of the area

Up until the termination of field work at the end of 1983, these marked lions had been tracked a total of 719 times. Subsequently, various assistants continued with the work on a sporadic basis and they were eventually tracked a total of 920 times. Additionally, some of the marked prides were followed (with the aid of the telemetry equipment) by two teams of photographers with the aim of compiling photographic material for films and books and both of these teams kindly supplied data on the kills made by these lions as well as on pride movements, structure and home range (Aiken *in litt*; Hughes, *in litt.**).

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* Aiken, B. 16 B Montezuma, 117 Snell Parade, Durban, 4001.

Hughes, D. Private Bag X405, Skukuza. 1350.

Figure 5.3.5 is a synthesis of all the available distribution and movement data to indicate home ranges of the various prides. The term "home range" is used here in preference to "territory" which implies active defence of the whole area and, although territories are defended by pride lions, the peripheral points indicating the extremities of the home ranges used by each pride are usually in areas of overlap with neighbouring prides and it is doubtful if confrontations in these overlap areas would lead to active defence. Shaded areas on the map are thus mere convex polygons connecting the outermost localities at which respective prides were recorded and do not show "core" areas (Figure 5.3.6) which are more important to each pride and which are relatively discrete. These convex polygons, however, do show that areas used by various prides provide a complete coverage of the total available area and thus from the point of view of a predator-prey study, preference ratings can be relatively easily calculated from the total number of lions and prey respectively from the whole area. Table 5.3.9 lists some of the information relevant to these prides.

Table 5.3.9: The marked lion prides showing pride sizes, number of marked animals, number of resightings and the home range size of each pride.

Pride No.	Pride name	Pride size			No. of marked animals	Total no. of re-sightings	Home range size (km²)
		M	F	Tot.			
1	Matikiti	3	5	10	1 (f)	64	69
2	Winkelhaakspruit	2	6	8	1 (m)	28	75
3	Satara	4	10	14	2 (f)	85	130
4	Sweni	3	10	13	3 (1m + 2f)	277	98
5	Confluence	2	10	12	4 (1m + 3f)	214	188
6	Makonkolwene	10	4	14	2 (m + f)	137	186
7	Tshokwane	2	2	4	1 (m)	32	100
8	Guwene	-	4	4	1 (f)	26	84
9	Lindanda	-	1	1	1 (f)	26	39
10	Campsite	4	-	4	2 (m)	31	88
	Total	32	52	84	-	920	703

Note (a) Pride number refers to the number in Figure 5.3.5.

(b) Pride size includes adults and sub-adults and is the maximum number of these two age classes in each pride recorded during the study.

(c) Number of marked animals also refers to the maximum number in the pride at any time during the study. Some marked lions changed prides and therefore the sum of the marked animals in this column (n = 18) does not equal the number of marked lions given elsewhere in the text (n = 15). The sex of the marked lions is given by (m) or (f).

(d) Home range size is calculated from the area of the convex polygons shown in Figure 5.3.5. Total home range is the area of the shaded area in Figure 5.2.1 which encompasses all the marked lions' home ranges.

A brief summary of the structure and of changes in the structure of respective prides is given below.

1. Matikiti pride. This pride was seen a few times early on in the study in the Sweni bridge area but was considered to be too far to the west to warrant marking. Later in the study when more radio collars had been obtained, a sub-adult female (3,5 years old) was fitted with a collar on 19 June, 1983. At that time the pride consisted of three adult females, 2 sub-adult females and two sub-adult males. Three adult males were later seen with this pride and

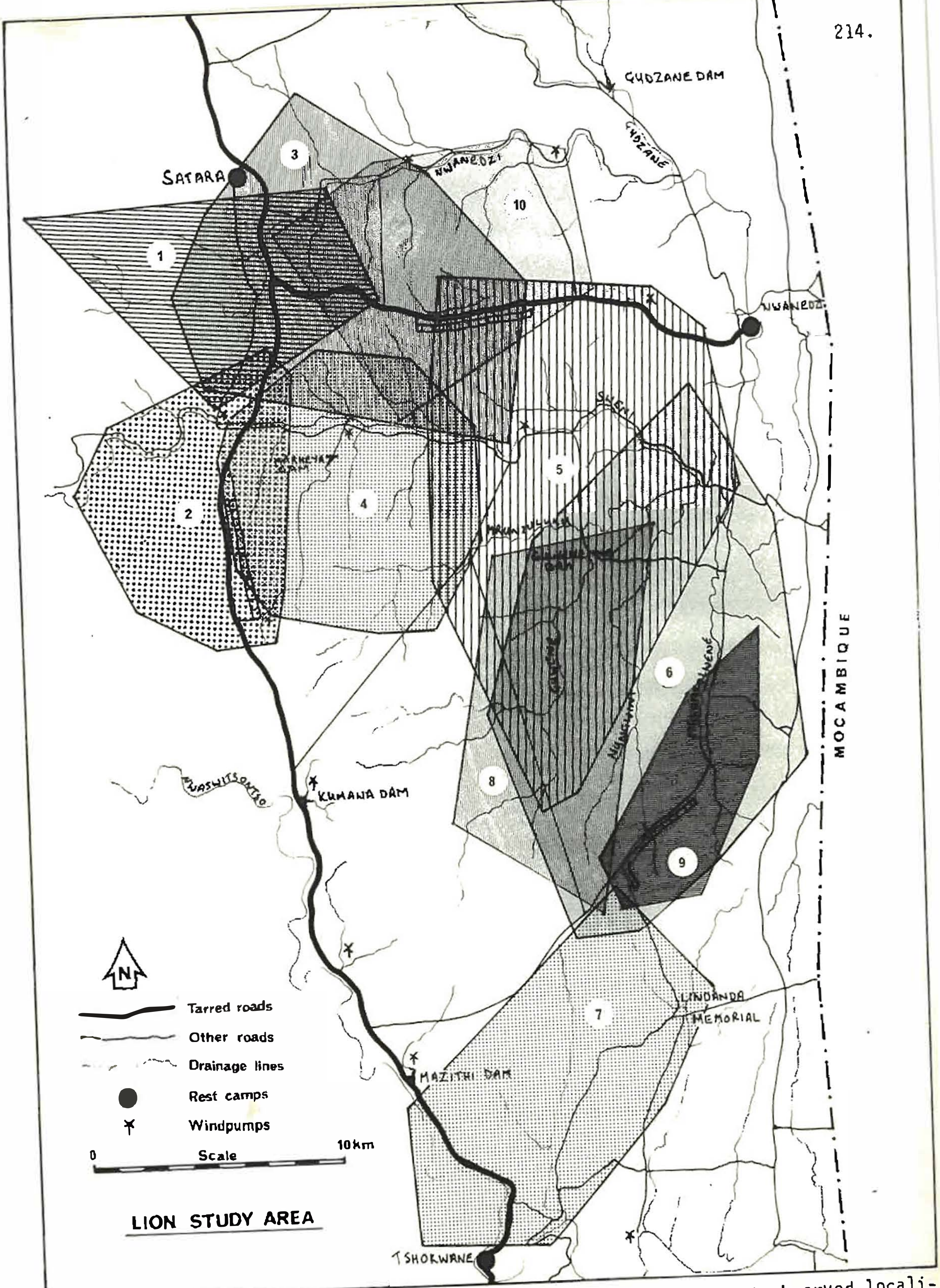

FIGURE 5.3.5: Convex polygons connecting the outermost observed localities of lion prides tracked by means of radio telemetry indicating the home ranges of respective prides in the lion study area.

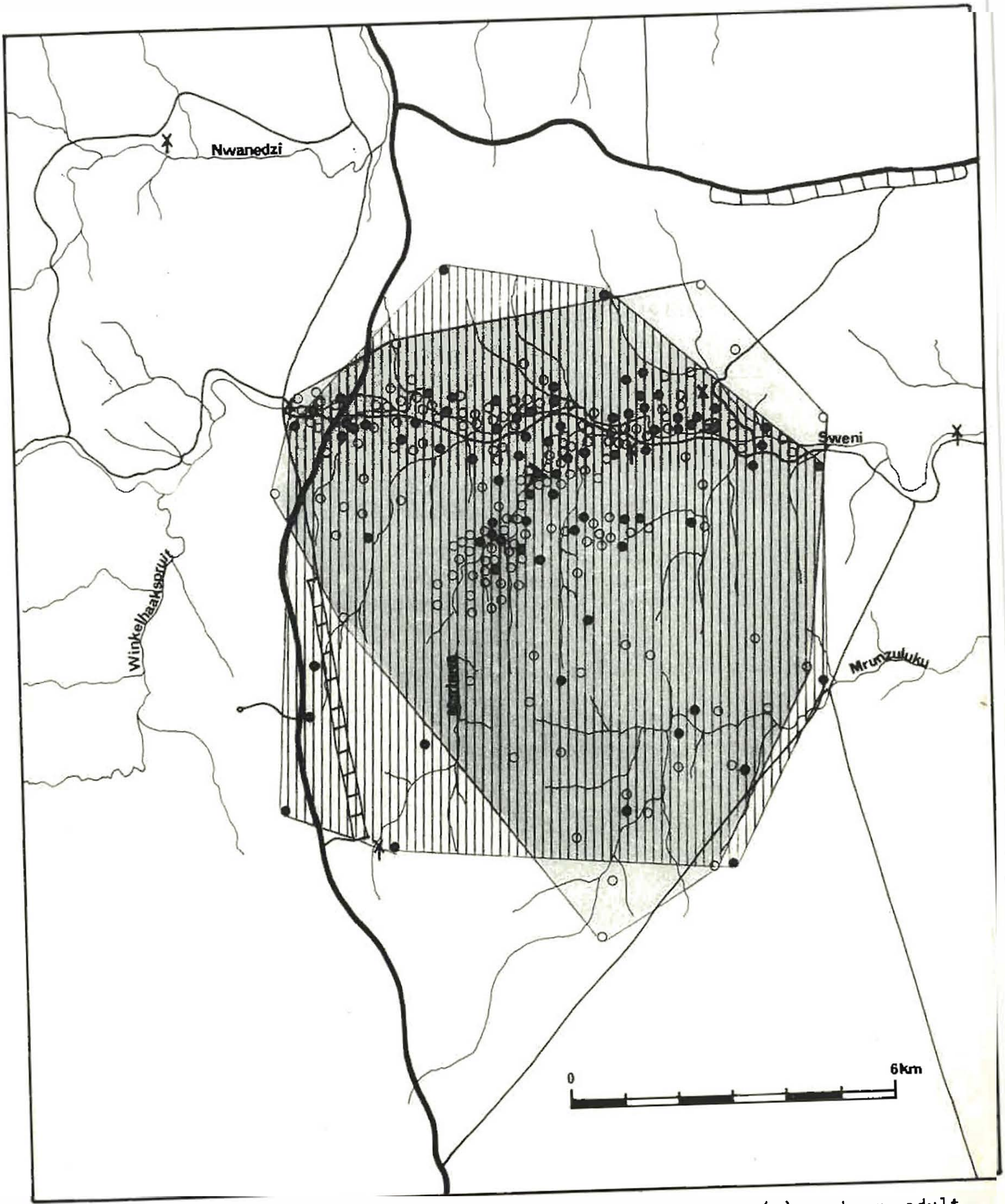

FIGURE 5.3.6: Localities where an adult male lion (•) and an adult female (o) of the Sweni pride were recorded by means of radio telemetry. The home ranges are shown for each by means of convex polygons connecting outermost localities and the high density core areas are evident.

the adult females were seen with 12 cubs (3 months old) on 1 April 1984. This was also the last date that the sub-adult males were seen with this pride. The two sub-adult females stayed with the pride however, and the marked female was found with her first litter (very small cubs) on 6 June. She apparently lost these cubs as they were not seen again. The last time the other females were seen with their cubs there were only seven left (10 July, 1984). After this, only sporadic contact was made with this pride and on these occasions, structure could not be ascertained. For the majority of the time therefore, the pride consisted of three adult males, 2 sub-adult males, five adult/sub-adult females and varying numbers of cubs (which need not be considered for further predator prey analyses).

As was suspected, this pride's home range proved to be too far west and thus out of the area in which summer aerial surveys were conducted. Regular tracking commenced late in the study and due to these two factors, relatively little data was obtained from this pride.

2. Winkelhaakspruit pride. As in the previous case, this pride's home range was too far west for regular tracking. It had not been intended to mark an animal from this pride, but the adult males from the Sweni pride (including the marked one) switched prides in August, 1983, and in order to maintain contact with these two males, they were tracked occasionally and incidental information was also gained on this pride. The structure of this group was two adult males, 6 adult or sub-adult females and a maximum of nine cubs.

3. Satara pride. A young female from this pride was first marked on 17 February 1982 on the Sweni spruit. Later, on 8 December 1982 a second young female in a sub-group from this pride was also marked. Structure of this pride during this period was five adult females, five sub-adult females and four sub-adult males. In February 1983, a group of five sub-adult females (including both marked lions) and one old adult female left the pride and became nomadic for a short while until May 1983 when all six were accepted into the Confluence pride. Contact was thus lost with the Satara pride and they were not seen again.

4. Sweni pride. Contact was initially made with this pride in September 1981 in an initial survey of the lions of this area. At this time the pride consisted of three adult males, five adult females and nine cubs (about one year old). A male and a female from this pride were then collared in December 1981 by which time there were only two adult males, four adult females and seven cubs left. This structure remained unaltered until August 1982 when two of the females (one of which was radio collared) produced new litters of three and four cubs respectively. Soon after this (November) the other two females and six of the seven cubs of the previous litters (by then sub-adult) became nomadic and the pride split up. The nomads disappeared from the area but returned during September 1983 and established themselves as a separate sub-group of the pride. The two males also broke away from the pride in March 1983 and established themselves as pride males of the Winkelhaakspruit pride. After this the two remaining females and the one remaining sub-adult female struggled to kill enough to maintain the group and all of the cubs died.

5. Confluence pride. Although this pride was seen on a number of occasions, it was not until April 1983 that they could be successfully captured. An adult male and female were then fitted with radio collars. At this time the pride consisted of two adult males, four adult females and one cub. During the following month they accepted six nomadic females into the pride. These females were all originally from the Satara pride. One of these females was fairly old and the other five were just attaining adulthood. The pride thus consisted of two adult males and 10 adult females. All or most of these females subsequently produced cubs and just over a year and a half later the pride consisted of two adult males, 10 adult females, 13 large cubs (1-2 years old), 10 cubs (6 months old); one cub (5 months old) and 4 cubs (3 months old), giving a total of 40.

6. Makonkolwene pride. This pride was also captured and marked in September 1981 during the initial survey of the area. At this stage the pride consisted of four adult males and four adult females. An adult male and an adult female from this pride were marked in December 1981 by which time the pride consisted of three males and three females. All of the females were lactating and had eight small cubs between them. This composition stayed unaltered until October 1983. The cubs (seven males and one female) were sub-adult by then and had begun to break away from the pride being with the adult females on some occasions and away on others. Both radio collars then ceased to function and contact

was lost with them but the young males stayed in the area and by may 1985 were challenging the Confluence pride males for tenure of that pride (Hughes, in litt.*).

7. Tshokwane pride. One of two adult males from this pride was marked on the Lindanda Plains in December 1981. These males' home range extended down to Tshokwane and was thus outside the area of interest in this study and so relatively few sightings were obtained of them. Their range coincided almost exactly with that of a large group of females and cubs which were well known to the Ranger of the area (Wolff, pers. comm**) due to the fact that a white cub was born in a litter in this pride. I did not ever record the two males in the company of this pride and I only twice recorded them in the company of other lions (two females). Wolff (pers. comm.) however, saw them with this pride on a few occasions and there seems little doubt that they were in fact the pride males of this pride. Wolff recorded the pride structure in 1982 as two adult males, six adult females and 12 cubs (seven males and five females). In September 1982 however, these two males were evicted from their home range and moved even further south into the Mlondozi area and I removed the collar on 20 October 1982.

8. Guwene pride. This pride consisted of only four adult females, one of which was marked in December 1982. They were once recorded

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* Hughes, D. Private Bag X405, Skukuza, 1350.

** Wolff, P. Senior Ranger, Tshokwane Section, Private Bag X402, Skukuza, 1350.

in the company of the Makonkolwene males but did not seem to have their own pride males. The marked female produced two litters of cubs and one other female produced one litter all of which died. This pride also contracted some form of mange in July 1983 from which they had all recovered clinically by December. One female was found dead at a wildebeest kill in December but the other three remained together until the collar ceased to function in January 1984 after which contact with them was lost.

9. Lindanda pride. Although referred to here as a "pride" there was in fact only one female in this group. She was recorded with the Makonkolwene males on three occasions but on all other sightings she was on her own. As her range fell almost entirely within the range of the Makonkolwene pride, it is probable that this female was the one that disappeared from the pride between September 1981 (when the pride was located during the initial survey) and December 1981 when the pride was captured for the fitting of radio collars. She was marked in April 1983 and last seen in July 1984 after which no further signal could be received from her collar. She produced two litters of cubs, the first of which she lost and the other was still with her at her last sighting.

10. Campsite pride. Two young adult males were marked from a group of four males. All of these males were immobilised but one of them unfortunately died during this capture process. They were in the Sweni pride's territory and as this pride had lost its males it was thought that these young males might take over the pride tenure. Subsequent to marking in October 1983 however, they moved north to

the Nwanedzi River. As they were largely outside the area of interest they were seldom tracked. They were not ever recorded in the company of other lions, and should actually be considered as nomads. One of the collars malfunctioned after only three months and the other collared lion was destroyed by National Parks Board officials in September 1984 as he had been paralysed in the hindquarters in a fight with other lions.

The structure of these prides is summarised below in Table 5.3.10 to assist with the analysis in the subsequent section.

Smuts (1978a) gave the structure of five of these prides (data from other prides were not given) as they were recorded in 1976. His data for these prides and those for the 1982/83 period of this study are given for comparison in Table 5.3.11.

The total number of lions in these prides for each period was identical but as the number of cubs is extremely variable due either to high mortality rates (vide the death of all seven cubs of the August 1982 litters of the Sweni pride) or high birth rates (vide the 28 cubs produced by the Confluence pride between 1983 and 1984), cubs should not be included in analyses of pride sizes. Chi-squared contingency table tests could show no difference in the total number of adult and sub-adult lions in these five prides between 1976 and 1982/83 (χ^2 = 5,36; d.f. = 3; $p > 0,1$). This suggests that the population of the area has remained reasonably stable over the period.

Table 5.3.10: Summary of the structure of respective prides in the study area for each year between 1981 and 1984.

Pride	Year	Adult*		Sub-Ad.*		Total Ad. + Sub. Ad.	Large cub*	Small cub*	Total (all ages)
		M	F	M	F				
Matikiti (1)	1982	-	3	2	2	7	-	-	7
	1983	-	3	2	2	7	-	-	7
	1984	3	5	-	-	8	-	7	15
Winkelhaakspruit (2)	1983	?	6	?	?	?	?	?	?
	1984	2	6	-	-	8	-	9	17
Satara (3)	1982	-	5	4	5	14	-	-	14
	1983	?	4	?	?	?	?	?	?
Sweni (4)	1981	3	5	-	-	8	-	9	17
	1982	2	4	-	-	6	7	0	13
	1983	-	2	-	1	3	-	/	10
	1984	-	4	1	6	11	-	4	15
Confluence (5)	1982	2	4	-	-	6	-	1	7
	1983	2	10	-	-	12	1	5	18
	1984	2	10	-	-	12	6	22	40
	1985	2	10	-	-	10	9	7	28
Makonkolwene (6)	1981	3	3	-	-	6	-	8	6
	1982	3	3	-	-	6	8	-	14
	1983	3	3	7	1	14	-	-	14
Tshokwane (7)	1981	2	2	-	-	2	-	-	2
	1982	2	2	-	-	2	-	-	-
Guwene (8)	1982	-	4	-	-	4	-	3	7
	1983	-	4	-	-	4	-	-	4
Lindanda (9)	1983	-	1	-	-	1	-	-	1
	1984	-	1	-	-	1	-	4	5
Campsite (10)	1983	4	-	-	-	4	-	-	4
	1984	3	-	-	-	3	-	-	3

* Adult = 4+ years old
Sub-Adult = 2-4 years old
Large cub = 1-2 years old
Small cub = 0-1 years old.

Table 5.3.11: Comparison between the structure of certain prides in the lion study area between 1976 (Smuts, 1978a) and 1982/83.

Sex and age class	Pride											
	Tshokwane (16)*		Guwene (18)		Makonkolwene (20)		Confluence (21)		Sweni (22)		Total	
	76	82/3	76	82/3	76	82/3	76	82/3	76	82/3	76	82/3
Adult M	1	2	6	-	2	3	1	2	5	2	15	9
" F	4	6	6	4	3	3	2	10	5	4	20	27
Sub-Ad. M	-	-	4	-	2	7	9	-	-	1	15	8
" F	-	-	2	-	3	1	6	-	-	6	11	7
Large cub	6	-	-	-	-	-	-	1	-	-	6	1
Small cub	7	12	-	3	5	-	-	5	-	7	12	27
Total	18	20	18	7	15	14	18	18	10	20	79	79

* Numbers in brackets are Smuts' pride numbers.

5.3.4.2 The prey in the area

Kill data from marked prides were collected for the years 1982-1984 and these data have been analysed for preference ratings. Data from six aerial ecological surveys are available for this period. These are: 1982 - summer and winter; 1983 - summer and winter; 1984 - summer and winter. Data for winter counts are from Joubert (1982, 1983 & 1984). Summer counts are from my own unpublished data. These data are given below in Table 5.3.12 as are the relative abundances (frequencies) of the individual prey species. Only eight species have been included as they form the only species of importance in the lions diet. Others are either too large (e.g. white rhinoceros), too small (e.g. steenbuck) or too rare (e.g. reedbuck) to represent a contribution to preference rating analysis.

Table 5.3.12: The numbers and relative proportions of eight prey species of lions in the Sweni/Lindanda area of the Central District obtained from aerial survey data between January 1982 and July 1984.

Prey species	Year											
	1982				1983				1984			
	January		July		January		July		January		July	
	No.	Rel. freq	No.	Rel. freq	No.	Rel. freq	No.	Rel. freq	No.	Rel. freq	No.	Rel. freq
Wildebeest	2239	27,9	2037	27,0	922	34,9	1538	33,8	2144	24,9	1455	29,1
Zebra	3317	41,3	1446	19,2	827	31,3	520	11,4	3431	39,0	660	13,2
Kudu	91	1,1	237	3,1	26	1,0	90	2,0	86	1,0	172	3,4
Impala	1426	17,8	3127	41,5	644	24,4	2061	45,3	2452	27,8	2098	41,9
Waterbuck	41	0,5	87	1,2	46	1,7	71	1,6	96	1,1	106	2,1
Giraffe	119	1,5	178	2,4	97	3,7	137	3,0	316	3,6	276	5,5
Buffalo	706	8,8	303	4,0	47	1,8	69	1,5	239	2,7	140	2,8
Warthog	83	1,0	126	1,7	34	1,3	60	1,3	41	0,5	100	2,0
Total	8022		7541		2643		4546		8805		5007	

It must be remembered that these totals merely represent the total number of each species seen during the respective counts and are thus a reflection of what was in the area at that time. The biases and assumptions that are inherent in this type of count have been discussed earlier and need not be repeated here. Also the boundaries of the area censused are not physical barriers and therefore movement in and out of the area is inevitable and may have an effect on respective count totals. The small though significant differences between respective summer and winter totals of wildebeest (total for all summers = 5 305; total for all winters = 5 030; χ^2 = 7,31; $p < 0,01$) are confusing. The majority of wildebeest in this sub-population are migratory, spending the summers in the north of their range (i.e. in the lion study area) and the winters in the south around Mlondozi. This is not reflected in these census totals as the migration of this species is dependent on rainfall and the availability of surface water (Smuts, 1972; Braack, 1973) and this influenced the results obtained during the various aerial surveys. In all of the winter (July) counts given in Table 5.3.12 the wildebeest totals appear to be too high while the January 1983 wildebeest total is far too low to be representative of the summer total for the area. As has been said earlier, early 1983 was exceptionally dry and by the January count the wildebeest had not yet moved into the area. The total of 922 is probably representative of the total remaining in the area during winter after all the migrants have left, while the July counts were still encountering migrants in the area who had not yet moved south. These seasonal totals must have affected the analyses accordingly and may have been the reason that no significant differences could be shown to exist between summer and winter data. However, the majority of the species are relatively sedentary (excluding wildebeest and zebra) and the relative proportions of these species in the area given by the previous table are probably sufficiently accurate for the purpose of these analyses. Population totals from aerial survey data were also used in determining preference ratings in the kill sample extracted from Rangers' returns, and the preference ratings obtained by the two different methods are thus comparable.

The extremely low totals of all species obtained during the January 1983 count was due to very little rain having fallen in the area. This was a particularly local phenomenon as the Rangers' stations as close by as Satara, Nwanedzi and Tshokwane had had some reasonable showers by then, and even some of the more sedentary species had obviously undertaken some local movement to more lush areas close by. In spite of the reduced number of all species, their relative proportions in the prey community remained much the same.

5.3.4.3 Kills found and preference ratings.

In total 121 kills were located by means of radio telementry between December 1981 and December 1984. Of these, 117 were of the eight major prey species given in Table 5.3.13 while the rest were one each of baboon (Papio ursinus), porcupine (Hystrix africaeaustralis), white tailed mongoose (Ichneumia albicauda) and spotted hyaena. Other kill data supplied by Aiken (in litt.*) and Hughes (in litt.*) were derived by following a single pride continuously for varying lengths of time. They have not been included in this sample due to this difference in the sampling method, but are given later in this section for comparative purposes.

Kill samples from individual prides were too small for separate analysis and have been pooled for respective summer and winter seasons during the study period. (Summers are considered to extend from October to March and winters from April to September).

Table 5.3.13: The kills of lion prides located by means of radio telemetry and the season in which they were made.

Prey species	Sum. 81/82	Win. 1982	Sum. 82/83	Win. 1983	Sum. 83/84	Win. 1984	Sum. 1984	Total		
								Sum.	Win.	Tot.
Wildebeest	3	4	9	5	2	9	1	15	18	33
Zebra	2	2	-	4	1	2	-	3	8	11
Buffalo	6	4	9	5	10	2	1	26	11	37
Giraffe	1	1	1	-	-	-	-	2	1	3
Warthog	4	3	-	2	-	1	-	4	6	10
Waterbuck	1	2	-	-	-	2	-	1	4	5
Impala	1	1	1	3	-	2	-	2	6	8
Kudu	-	1	4	2	3	-	-	7	3	10
Total	18	18	24	21	16	18	2	60	57	117

* See footnote on page 210.

Due to the influx of migratory wildebeest in summer it was expected that there would be a concomitant increase in the proportion of wildebeest in the lions' diet. This was not supported by the data, and in fact more wildebeest kills were found in winter (n = 18) than in summer (n = 15), though this could not be proven significantly (χ^2 = 0,342; $p > 0,5$).

Wildebeest featured prominently in the diet of the lions of this area, making up 33 of the 117 kills found (28,2%). This was only exceeded by buffalo (37 kills - 31,6% of the sample). Preference ratings were also calculated for these kill data and the calculations follow the method of Pienaar (1969b). Kill data for the summers and winters of respective years have been combined due to small sample sizes and therefore the census data from these years also had to be combined and the means of these seasonal totals are given in Table 5.3.14.

Table 5.3.14: Preference ratings of eight prey species of lions calculated for summer and winter periods from aerial survey data and data on lion kills located by radio telemetry.

Season	Parameter	Wildebeest	Zebra	Buffalo	Giraffe	Wart-hog	Water-buck	Impala	Kudu	Total
Summer	No. kills	15	3	26	2	4	1	2	7	60
	Rel.freq.	25,0	5,0	43,3	3,3	6,7	1,7	3,3	11,7	-
	Census	1768	2525	331	177	53	61	1507	68	6490
	Rel.freq.	27,2	38,9	5,1	2,7	0,8	0,9	23,2	1,0	-
	Pref.rat.	0,91	0,13	8,50	1,22	8,16	1,77	0,14	11,13	-
Winter	No. kills	18	8	11	1	6	4	6	3	57
	Rel.freq.	31,6	14,0	19,3	1,8	10,5	7,0	10,5	5,2	-
	Census	1677	875	171	197	95	88	2429	166	5698
	Rel.freq.	29,4	15,4	3,0	3,5	1,7	1,5	42,6	2,9	-
	Pref.rat.	1,07	0,91	6,43	0,51	6,31	4,54	0,25	1,81	-
Total	No. kills	33	11	37	3	10	5	8	10	117
	Rel.freq.	28,2	9,4	31,6	2,6	8,5	4,3	6,8	8,5	-
	Census	3445	3400	502	374	148	149	3936	234	12188
	Rel.freq.	28,3	27,9	4,1	3,1	1,2	1,2	32,3	1,9	-
	Pref.rat.	1,00	0,34	7,68	0,84	7,04	3,50	0,21	4,45	-

It must be remembered that the preference ratings are calculated from the relative proportions of each species in both the census totals and in the kill sample. The actual number of kills found is therefore of little importance as long as the relative proportions of each species in the kill sample was representative of the proportions in which they were actually killed by lions. From the high proportion of impala in the stomachs of culled lions (40 out of 131 stomachs which contained prey remains were of impala (Smuts 1978 b,c)) and the low proportion of impala in the kills actually found (two out of 117 kills found), it can be concluded that impala are under represented in this (and other) kill samples ($\chi^2 = 16{,}3$; $p < 0{,}001$) and should probably be excluded from these analyses. However, removal of impala from the above table merely lowers the kill and census totals and all the other species preference ratings change proportionately which does not affect the results or conclusions drawn. The very low impala preference rating should, however, be seen as an under-representation. Similarly warthog are probably less visible from the air due to their small size and grey colour and they are probably under-represented in the census totals which would lead to a disproportionately high preference rating.

In spite of the high proportion of wildebeest recorded in the diet of these marked prides (28,2% of all kills) their preference ratings are relatively low which is due to their abundance in the area. This low preference rating is to be anticipated as the study area contains the prime wildebeest habitat of the summer grazing area and it is to be expected that vulnerability to predators will be low in prime habitats. This is also prime habitat for zebra and this is also reflected in their low preference ratings.

The kill data suppled by Aiken (in litt*) and Hughes (in litt*) are given in Table 5.3 .15. Kill data from this study are also given for comparison. The data from the various sources in this table was derived in two different ways. Methods for this study have been described. The data of Aiken and Hughes were obtained by following the Confluence pride at night and directly observing its kills. This pride was selected due to its exceptional size at the time (approximately 40 individuals) which greatly enhanced its value for photographic purposes.

Table 5.3.15: Lion kills located by means of radio telemetry from this study, from Aiken (August 1984-January 1985) and from Hughes (February 1985-June 1985).

Species	Data source							
	This study		Aiken (A)		Hughes (B)		A + B	
	No. kills	Rel. freq.	No. kills	Rel. freq.	No. kills	Rel. freq.	No. kills	Rel. freq.
Wildebeest	33	28,2	37	61,7	14	36,8	51	52,0
Zebra	11	9,4	5	8,3	15	39,5	20	20,4
Buffalo	37	31,6	1	1,7	1	2,6	2	2,0
Giraffe	3	2,6	2	3,3	1	2,6	3	3,1
Warthog	10	8,5	2	3,3	3	7,9	5	5,1
Waterbuck	5	4,3	3	5,0	-	-	3	3,1
Impala	8	6,8	9	15,0	4	10,5	13	13,3
Kudu	10	8,5	1	1,7	-	-	1	1,0
Total	117	99,9	60	100,0	38	99,9	98	100,0

The proportions of the various prey species in these three samples showed considerable variation. The proportion of wildebeest in this study's kill sample differed significantly to that of the combined samples of Aiken and Hughes (χ^2 = 11,74; $p<0{,}001$). This suggests that

* See footnote on page 210.

the different sampling techniques may have rendered different results. However, the proportion of wildebeest in this study's sample differed significantly to that of Aiken (χ^2 = 16,3; $p<0,001$) but not to that of Hughes (χ^2 = 0,645; $p>0,1$). Hughes' data also differed significantly in this proportion to that of Aiken (χ^2 = 4,793; $p<0,05$) which means that it was seasonal changes in the Confluence pride's diet and not differences in the sampling technique which gave rise to the proportional differences in the kill samples. Aiken's period of study was in the summer when the migratory wildebeest ought to have been in the area while Hughes was active from the late summer to the middle of winter by which stage the wildebeest should have left, and hence the reduced proportion of wildebeest in Hughes' sample. This is not corroborated by the increase in the proportion of zebra in Hughes' sample as this species migratory patterns should conform to those of the wildebeest. However, no census data are available for this area for this period and so no definite conclusions can be drawn.

It was shown in Chapter 4 that many of the adult wildebeest bulls remain on their territories in the lion study area during winter while the rest of the sub-population move to the south of their range. It could therefore be expected that the sex ratio (cows per bull) of the sub-sample of wildebeest killed in summer would be greater than in winter when cows were scarcer. Table 5.3.16 gives the age and sex of wildebeest killed in summer and winter.

No calf kills were located and yearlings are also not represented in this table. Of the seven kills whose ages or sexes were unknown (due to skulls missing) four were probably yearlings, though this could not be established with certainty.

Table 5.3.16: The ages and sexes of wildebeest killed by lions located by means of radio telemetry according to the season in which they were killed (Summer = October-March; Winter = April-September).

Season	Bulls			Cows			Unknown
	Adult	Yearling	Calf	Adult	Yearling	Calf	
Summer	7	-	-	3	-	-	3
Winter	10	-	-	6	-	-	4
Total	17	-	-	9	-	-	7

The 17 bulls and nine cows killed did not represent a significant departure from parity (χ^2 = 2,46; p>0,1), and no difference could be detected between the sex ratios of wildebeest killed in summer and winter respectively (χ^2 = 0,001; p>0,5). This may be ascribable to the small sample size.

Unfortunately the nature of the work of Aiken and Hughes did not allow for more detailed observations and thus the ages and sexes of wildebeest killed could not always be recorded and their data could not be included in these analyses. Therefore from this part of the study, no significant conclusions can be drawn regarding the sexes and ages of wildebeest killed by lions.

Although all of these other species had to be included in Table 5.3.14 to enable the calculation of preference ratings for wildebeest, a full analysis of the predator-prey relationships of lions with all of these species is not relevant here, as it was the objective merely to attempt an assessment of the impact of lions on the wildebeest population. But as these preference ratings are a useful index of the vulnerability of each species to the predator concerned, some discussion of the other species is required.

The high proportion of buffalo in this kill sample is an unusual feature of this study as in all other predator-prey studies undertaken in the KNP, buffalo have not constituted a prominent prey item of lions. Pienaar (1969b) found buffalo to be the lowest numerically in his sample from Rangers' returns (5,8%), while from the same source Smuts (1975b) found them to be the fourth of the seven species he considered (9,3%). From the analysis of 252 culled lions' stomach contents, Smuts (1978b, c) found buffalo in only 2,3% - also the lowest in the sample and Bryden (1976) recorded no buffalo in a sample of 41 kills from his study area to the north-west of Satara between 1971 and 1973.

The reasons for the high proportion of buffalo in this study's kill sample are not clear. The very dry period in early 1983 led to some mortalities due to starvation among buffalo in the area at that time and some of those in a weaker condition were killed by lions, but from Table 5.3.13 it can be seen that buffalo kills were not restricted to this period but were fairly evenly spread over the whole study period. However, the preference ratings calculated from Rangers' returns given in Table 5.3.2 also suggest that there had been an increase in buffalo predation from 1979 onwards. The preference rating in 1979 was 0,25 and rose steadily to 3,62 in 1983, while in this study it was calculated at 7,68 - the highest of all species. Census figures showed that 1979 was probably the nadir of the wildebeest decline which coincides with the initial increase in the preference rating of buffalo and this is probably indicative of prey switching by lions from wildebeest to buffalo.

Census totals of buffalo also show that the population (breeding herds plus bulls) declined between 1982 (11 481 buffalo) and 1983 (7 584). This trend continued into 1984 when 6 885 were counted. This decline cannot be ascribed to buffalo culling as only 1 496 and 296 were culled between 1982-1983 and 1983-1984 respectively. Declines recorded over these two respective periods were 3 897 and 699 which are respectively far greater than the numbers culled. It is known that some mortality occurred early in 1983 due to the extreme drought conditions (Anonymous, 1983; own observations) and this may have been responsible for the majority of the decline recorded during that year but conditions improved the following year and yet the population continued to decline in excess of the culling totals. The increase in the preference ratings of buffalo in the diet of lions suggests that these predators may have played a role in the decline in the buffalo population recorded over these two periods.

The extremely low proportion of buffalo in both Aiken's and Hughes' samples in comparison to that of this study (χ^2 = 29,5; $p<0,001$) may be attributable to seasonal scarcity of buffalo in this prides area but again no census data are available.

5.3.4.4 Kill frequency

Although during this study lion prides were not followed for continuous periods in order to observe their kills (and therefore also to determine kill frequency), it was possible to infer this kill frequency from an assessment of whether lions had recently eaten or not. The size and tautness of the abdomen was indicative of whether they had had a substantial meal the previous night though lions which had eaten only a little may not have been distinguishable from those that had had nothing. An adult wildebeest would constitute a substantial meal to a pride of a normal size but calves would probably not and would be under represented in a sample using this method. Schaller (1972) used this technique and from the proportion of lions which either had fed or were on a kill to those who were neither gorged nor on a kill, the kill frequency can be estimated. Between 1967 and 1968 Schaller classified 1 815 lions - 33% were on a kill or were gorged and 67% were neither and he concluded that lions had a major meal every third day. This method was also used during this study and although individual lions were not classified as having recently fed or not, each pride was examined when they were located and this assessment was made of its members. Of the total number of times that prides were tracked, it was possible on 498 occasions to assess whether they had recently killed and/or fed or not. This they were found to have done on 179 of these occasions or 35,9%. This means that on average these prides had had a substantial meal once every 2,78 days. A chi-squared contingency table test shows that this is not significantly different to Schallers' data (χ^2 = 1,38; $p > 0,1$).

Although both Aiken and Hughes supplied data on lion kills, Aiken unfortunately did not include the number of nights when the prides had no success so the pride's kill frequency could not be calculated. Hughes did supply this information and for the 46 nights during which he followed the Confluence pride they made 39 kills. This pride was still very large at the time however (10 adult females with approximately nine cubs (one year old) and seven cubs (six months old)), and many of the smaller kills (e.g. impala yearlings, porcupine pup, wildebeest calves, zebra foals) would not have made a significant meal for the whole pride. When these small kills (n = 15) were excluded from the sample, 24 substantial kills remained and were made during the 46 day period or one meal every 1,9 days. This is significantly different from my sample (χ^2 = 4,07; p<0,05). This difference is undoubtedly due to the large pride size as even an adult wildebeest or zebra would not go far between that many lions. Thus they would have to kill more regularly than a small pride who would have been able to gorge themselves on a kill of that size and not have to kill again for a few days or more. This was partially substantiated by Aiken (pers. comm.) who informed me that while he was working on the Confluence pride they were for a time "killing a wildebeest every night". At this time the pride was at least 40 strong (Table 5.3.10) and competition at kills amongst pride members was very fierce.

To test this hypothesis that larger prides kill more often than smaller ones, the kill frequency was calculated for each pride according to the method above and an average size for each pride calculated. These calculations are given in Table 5.3.17. Pride size is given in "lion-units" where an adult female was regarded as one "lion unit". Two adult males were considered to constitute three lion units, sub-adults to one lion unit each and large cubs (between one and two years old) at four cubs to one lion unit. Smaller cubs (less than one year old) were ignored. This was rounded to the nearest whole number. Pride sizes were taken from those given in Table 5.3.10.

Pride sizes have been plotted against kill frequency in Figure 5.3.7 and the negative correlation between these two variables is clear. A least squares regression line (y = 22,5 - 4,31x) was fitted to the data points and a linear regression test on r X 2 contingency tables (Steele & Torrie, 1980) proved a significant relationship between the two (χ^2 = 85,75; d.f. = 1; p<0,001). Bryden (1976), however, working

Table 5.3.17: The frequency (mean no. of days between kills) at which lion prides kill in relation to pride size in "lion units" (see text).

Pride	Year	Pride size (lion units)	No. times tracked	No. times killed or eaten	Kill frequency
Matikiti	83/84	8	29	10	2,90
Satara	82	14	54	20	2,70
Sweni	82	9	76	25	3,04
Sweni	83	3	68	15	4,53
Sweni	84	3	43	11	3,91*
Confluence	83/84	13	80	30	2,60
Confluence	84	16	?	?	1,00**
Confluence	85	15	24	15	1,92***
Makonkolwene	82	9	30	9	3,33
Makonkolwene	83	15	30	15	2,31
Tshokwane	82	3	22	6	3,67
Guwene	83	3	25	5	5,00
Lindanda	83/84	1	15	3	5,00

* Although Table 5.3.10 gives this pride's size in 1984 as 15, the collared animal was in a sub-group of two adult females and one sub-adult female. Only this latter group's kills are included as the other group was seldom seen.

** From Aiken (pers. comm.) see previous page.

*** Data from Hughes (*in litt.*)

on a single pride in the Satara area found that they killed 17 times out of 75 days or once every 4,4 days. This kill rate is significantly different to that calculated for this study (χ^2 = 4,53; p<0,05) and according to the equation fitted to the data points in Figure 5.3.7 his pride of two adult males, two adult females and seven large cubs (seven "lion units") should have killed at a rate of about once every 3,6 days. Sample variation due to his relatively short sampling period with data from a single pride only may account for this difference.

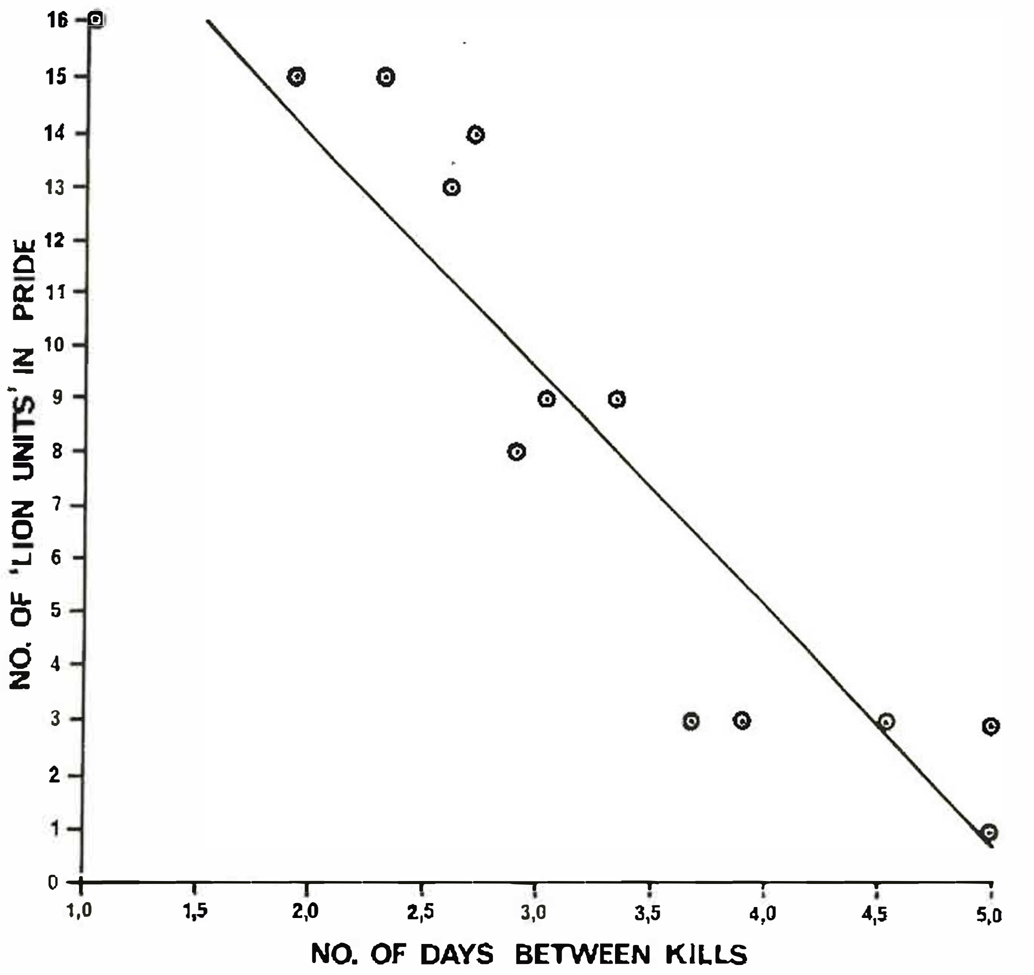

FIGURE 5.3.7: The relationship between lion pride size in "lion units" and frequency at which kills are made. See text for further explanation.

Thus although there was considerable variation between the kill frequencies of respective prides, the consensus between Schaller's results and those of this study suggest that an average rate of one large kill every third day per pride is applicable to both Serengeti lions and those in the CD.

5.3.4.5 The impact of lions on the wildebeest population.

As has been said earlier in this chapter, any calculation attempting to assess the impact of a predator on a prey population and based on data gathered by a study such as this one, must unavoidably make certain assumptions of dubious validity for the process of extrapolation.

During this study data were gathered on the kill frequencies of 10 prides and the relative species composition of their prey. Smuts (1976a, 1978a) estimated that there were 60 prides in the CD, of which 19 fall into the area of the Sweni/Mlondozi wildebeest sub-population. Thus data are available from 16,6% of the prides in the CD and from 52,6% of the prides preying on the Sweni/Mlondozi sub-population. It would be invalid to extrapolate the kill rates and species composition of the prey of the 10 study prides to the other 50 prides in the CD. Different landscapes have different densities of wildebeest and thus prides in other landscapes would not have access to the same proportion of wildebeest in spectrum of their home ranges' prey communities. Even the extrapolation of these data to the other nine prides which have access to the Sweni/Mlondozi sub-population may incorporate a compounded error in the sample, calculations or the logic of nearly 50%.

However, as the Sweni/Mlondozi sub-population is largely restricted to the fairly homogeneous Sclerocarya birrea/Acacia nigrescens savanna landscape (Figure 2.5.1), an assessment of the impact of lions on this sub-population has been attempted.

The distribution of lion prides in and around the lion study area does not appear to have changed since 1976 as each pride's home range as shown in Figure 5.3.5 conforms almost exactly to the locations given by Smuts (1976a). It has also been shown in this study that sizes of those prides on which data are available from both periods (Smuts, 1978a) have not changed significantly. For the purposes of this calculation therefore, it will be assumed that the number of prides (19) and their respective sizes have not changed. Smuts (1976a) calculated that these 19 prides totalled 246 lions of all ages. The proportions of each age class were adults - 50,4% at a sex ratio of 1 male to 2,4 females; sub-adults - 23,7%; large cubs - 10,8%; and small cubs - 15,1%. When reduced to actual numbers, this gives 36 adult males, 88 adult females, 58 sub-adults, 27 large cubs and 37 small cubs or 207 lion units. This gives a mean of 10,89 lion units per pride which, according to the straight line equation ($y = 22,5 - 4,31x$) fitted to kill frequency data points in Figure 5.3.17, should each have made a large kill once every 2,69 days on average, or 136 kills per year of which 19,4% were wildebeest in 1981/82, 31,1% in 1982/83 and 32,4% in 1983/84 (From Table 5.3.13). Thus these extrapolations suggest that 502 wildebeest from the Sweni/Mlondozi sub-population were killed by lions in the 1981/82 season, and 804 and 836 were killed in the 1982/83 and 1983/84 seasons respectively. These data are summarised in Table 5.3.18, and this sub-population's trends over the period are also given (from Table 4.3.9).

Table 5.3.18: The estimated number of wildebeest of the Sweni/Mlondozi sub-population killed by lions per year between the 1981/82 and 1983/84 seasons and the sub-population trend during that period.

Season	Total est. no. of kills made by lions	Est. proportion of wildebeest in total kills	Est. no. of wildebeest killed	Sub-population trend
1981/82	2 584	19,4	501	+437 (+16,5%)
1982/83	2 584	31,1	804	+226 (+ 7,3%)
1983/84	2 584	32,4	837	-309 (- 9,4%)

There was thus a negative correlation between the estimated number of wildebeest killed and the actual sub-population trend. The more wildebeest killed, the less the sub-population increased. Least squares regression analyses are not applicable to these data, but the method of Spearman's Rank correlation gave a coefficient of $r_s = -1{,}00$. The probability of this relationship could not be calculated due to the small sample size ($n = 3$). Based on these data then, there is tentative evidence that as lion predation increases the sub-population's growth rate decreases. Furthermore, if the recruitment (number of calves that could be expected to have been born) to this sub-population is compared to the expected number of wildebeest killed by lions during respective years the potential impact of lions can be illustrated. Table 5.3.19 gives these calculations.

Here again the limitations of the data need to be borne in mind and two of the major biases here are that:

a) Wildebeest calves are under-represented in the sample used to estimate the number of wildebeest killed per year and thus the actual number killed may be greater.

Table 5.3.19: The expected number of wildebeest killed from the Sweni/Mlondozi sub-population by lions compared to the expected number of calves produced during respective seasons.

Season	Cows counted *	Total w'beest counted *	% cows *	Sub-population size **	Est. no. of cows	Est. no. of calves +	Est. no. of w'beest kills ++	Proportion (%) of recruitment killed
81/82	325	906	35,9	2641	947	758	501	66,1
82/83	355	931	38,1	3078	1174	939	804	85,6
83/84	272	612	44,4	3304	1468	1174	837	71,3
Mean						957	714	74,6

* From January ground count data given in Table 4.3.12.

** From aerial survey data given in Table 4.3.9.

\+ From the 80% pregnancy rates given by Braack (1973).

++ From Table 5.3.18.

b) All of the 19 prides in this sub-population's area may not have access to the same proportion of wildebeest in their respective prey communities and thus the actual number of wildebeest killed may be lower than that estimated.

If it is assumed that these two sources of error negate each other, and that the estimated proportion of the annual recruitment killed is reasonable, then lions during the study period removed a mean proportion of 74,6% of the potential recruitment to the population which is very high when it is realised that other possible mortality factors have not been considered. These data were also gathered during a period of general increase in the wildebeest population and the potential impact must therefore be even greater during periods of decline.

5.3.5 Effects of predator culling

Predator culling was terminated in 1980 largely due to information gained through the ground counts described in Chapter 4. As these analyses have not been published in any form elsewhere and as they formed an integral part of this project in its early days, these analyses are given here in order to place them on permanent record.

As predator culling at the time was only practiced in the Sweni/Mlondozi sub-population's area, the other two sub-populations were available as "control areas". However, as the decline in the Western Boundary sub-population was induced by the boundary fence, and could therefore not be ascribed directly to predators, this sub-population's data could not be considered comparable and was not used. The Satara sub-population, however, was apparently subjected to the same pressures as those which had caused the decline in the Sweni/Mlondozi sub-population and could therefore serve as an ideal "control" for comparison.

Two parameters were used to assess the effect that predator culling would have on the wildebeest population. These were:

a) Cow/calf ratios as it was expected that calf survival rates would be greater in the sub-population benefitting from the predator culling.

b) The growth rates of each sub-population could also be compared as once again,the sub-population benefitting from the removal of predators could have been expected to have shown a higher growth rate.

The methods used for predator culling have been described by Smuts (1978a); Smuts, Whyte & Dearlove (1977, 1978) and need not be repeated here. Figures 4.1.1 and 5.2.1 indicate the area where predator culling was conducted. Tables 3.1.3 and 3.1.4 give the numbers of lions and hyaenas culled and Tables 4.3.20 and 4.3.21 give the cow/calf ratios recorded in the two sub-populations. Table 4.3.9 gives the sub-population totals recorded for respective years during aerial surveys.

The cow/calf ratios from respective calf cohorts from the two sub-populations were plotted graphically in Figure 5.3.8 for the three years in which both predator culling and ground counts were conducted (1978, 1979 and 1980). The number of lions and hyaenas culled and the times at which they were culled are also given. Least squares regression lines were fitted to these data to show their respective trends though once again further least squares correlation analyses are invalid on these data. Linear regression tests on r x 2 contingency tables (Steele & Torrie, 1980) were used on these data and the chi-squared values and probabilities are given in Table 5.3.20.

Table 5.3.20: Results from linear regression tests on r x 2 contingency tables on cow/calf ratio data from the Sweni/Mlondozi and Satara sub-populations from calf cohorts born in 1978, 1979 and 1980.

Sub-population	Year of birth	Equation	χ^2 value	Probability (df = 1)
Sweni/ Mlondozi	1978	y = 74,2 - 7,46x	79,55	$<$0,001
	1979	y = 75,4 - 7,41x	81,95	$<$0,001
	1980	y = 83,6 - 7,65x	63,88	$<$0,001
Satara	1978	y = 52,9 - 4,03x	16,33	$<$0,001
	1979	y = 64,7 - 6,28x	37,86	$<$0,001
	1980	y = 74,6 - 7,17x	53,24	$<$0,001

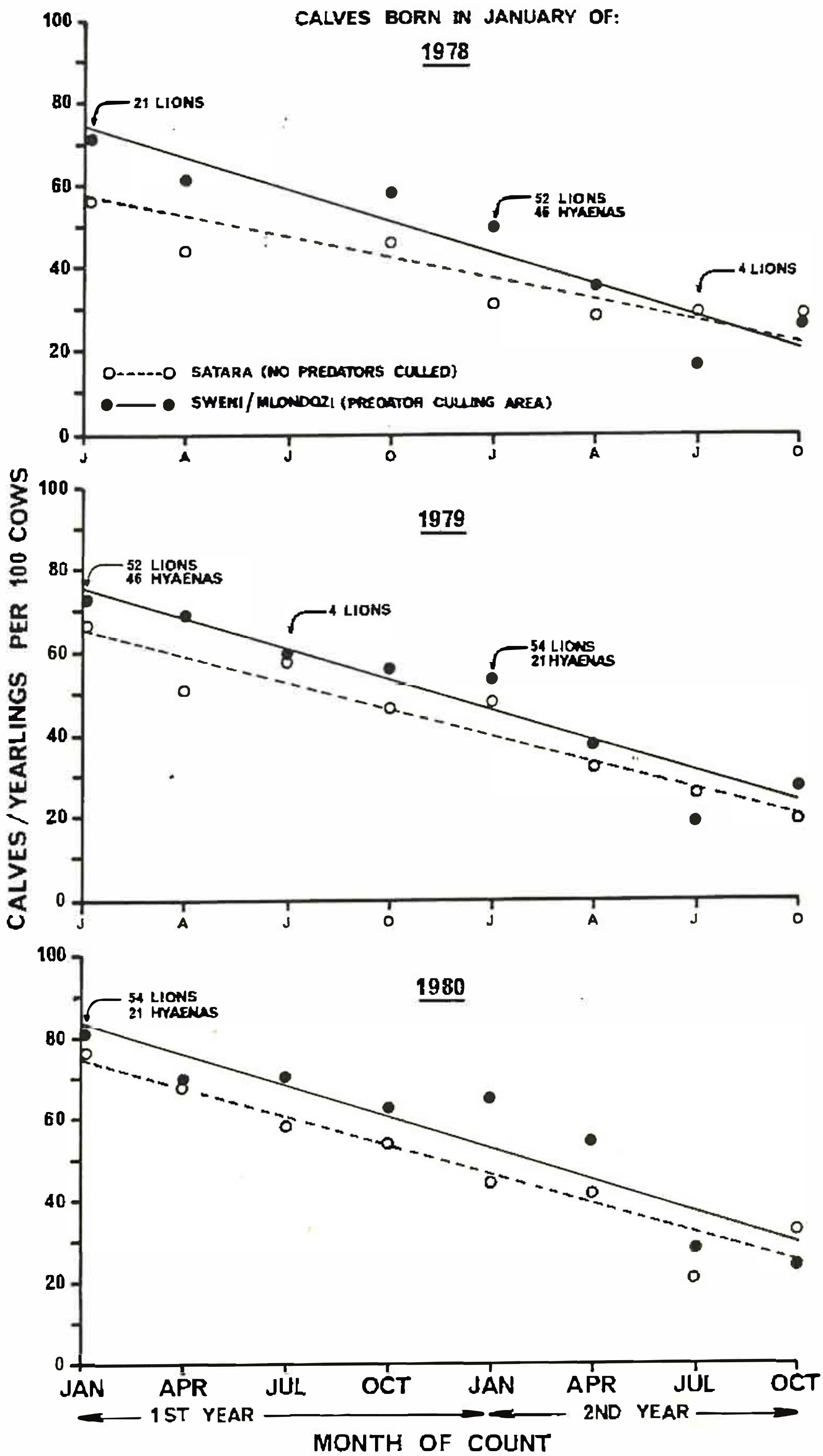

FIGURE 5.3.8: Cow/calf and cow/yearling ratios from the 1978, 1979 and 1980 calf cohorts of the Sweni/Mlondozi and Satara sub-populations where predator culling respectively had and had not been conducted.

It is clear that for all three calf cohorts, the early cow/calf ratios were higher in the Sweni/Mlondozi sub-population than in the Satara sub-population which infers that initially the predator culling was achieving one of its objectives - the relief of predator pressure on the newly born calves. But the two straight lines fitted to the data converge in all three cases showing that the initial advantage was lost as time progressed until at 21 months old, the cow/calf ratios were almost identical.

To test the significance of this convergence, the cow/calf ratios from each sub-population (given in Tables 4.3.20 and 4.3.21) were pooled for the first year (first four counts) and also the second year (remaining counts). Pooled data from the first year from each sub-population were tested against each other (chi-squared contingency table) as were those from the second year of life. Results of these tests are given in Table 5.3.21.

Table 5.3.21: Results of chi-squared contingency table tests on pooled cow/calf ratio data from the Sweni/Mlondozi and Satara wildebeest sub-populations where predator culling respectively had and had not been conducted.

Cohort born in:	First year						Second year					
	Sweni/Mlondozi		Satara		χ^2	p	Sweni/Mlondozi		Satara		χ^2	p
	Cows	Calves	Cows	Calves			Cows	Calves	Cows	Calves		
1978	634	410	445	216	129	<0,001	990	315	598	175	0,53	>0,5
1979	990	635	598	315	5,03	<0,025	1096	390	595	178	2,63	>0,1
1980	1096	780	595	372	2,43	>0,1	1207	567	785	257	16,54	<0,001

Thus in the 1978 calf cohort, the cow/calf ratios were significantly higher in the Sweni/Mlondozi sub-population during the first year of life than in the Satara sub-population but by the second year of life the difference had decreased so as to be not significant statistically. This trend was repeated by the 1979 calf cohort. The reason for this convergence of the cow/calf ratios is almost certainly due to the Sweni/Mlondozi wildebeest moving out of the predator culling area in winter and therefore being exposed to normal predator pressures in the other parts of their range. Thus, this sub-population spent almost half of its time outside the culling area and during that time the predators were able to reduce the cow/calf ratio to that of the Satara sub-population and ultimately, by the time the calves were 21 months old, no benefit had been gained from the culling of lions and hyaenas. The calf cohort of 1980 did not conform to this trend as the two sub-populations first year cow/calf ratios were not significantly different but the second year's ratios were. However, predator culling was only conducted during the time of birth of this calf cohort and not again during its first two years of life and the significant difference the two sub-populations' second year ratios can therefore not be ascribed to predator culling.

As for growth rates, Figure 4.3.5 shows that the trends followed by the two sub-populations were almost identical between 1978 and 1981 and no response to the predator culling is discernible on this graph. A chi-squared contingency table test conducted on the two sub-population's totals obtained from ecological aerial surveys (see Table 4.3.9) could also detect no significant differences (χ^2 = 2,66; d.f. = 3; $p > 0,3$).

5.4 CONCLUSIONS

5.4.1 Ranger's returns

Due to the inherent biases in this method of data collection, the data contained in Ranger's returns have always beeen treated with some scepticism by Research and Management staff in the KNP. Smaller species and calves are under-represented in these kill samples and therefore smaller species cannot be compared directly with larger ones. Also the methods of patrolling the respective Ranger's Sections are not consistent due to the different personal requirements of each Ranger, and because of the differing nature of tasks facing him and his staff which is largely dictated by the character and geographic location of the Section itself. However, if it is assumed that a carcass of a particular species, which has been killed by a particular predator, has the same probability of being found and that therefore the proportion of each prey species in the sample of found kills is relatively representative of the proportion that that species actually contributed to the particular predator's diet, then trends in the annual preference ratings may be indicative of changes in vulnerability to that predator or of prey switching as environmental changes occur. From the data presented in this thesis, this would appear to be a reasonable assumption as the trends in the wildebeest's preference rating conformed to the expected pattern - it increased as the population declined and then decreased markedly as the population recovered. Also some interesting relationships have emerged between wildebeest and waterbuck and between wildebeest and buffalo.

In the case of waterbuck, these data gave evidence of a shift in vulnerability to lion predation from one to the other, while in the case of buffalo evidence of actual prey switching from wildebeest to buffalo is given. This switch to buffalo must have eased pressure on the wildebeest population considerably and contributed significantly to the dramatic increase showed by the wildebeest population after 1979. These insights into these processes were derived purely from the data contained in the Rangers' monthly returns and much of the scepticism is therefore unfounded, and I propose that for the purposes of population monitoring of all the major prey species of lions, these data provide a useful extra perspective into the ecological processes which govern their dynamics.

5.4.2 Found wildebeest skulls

Three aspects of interest emerged from this sample of found skulls. The first was that mortality was higher in the male segment of the population at a younger age than in the female segment. Braack (1973) found that wildebeest in the CD were born at a 1:1 ratio and thus the early mortality in the bull segment obviously leads to the ultimate distortion in the adult sex ratio which was found to be an average of one bull to 2,02 cows from ground count data. Factors contributing to this early mortality were, however, not investigated.

Secondly, the population did not have a stationary age structure. Female skulls when separated into older (since death) and fresher sub-samples showed significantly different age distributions indicating that the age distribution had changed over time. Data from this skull sample were thus not suitable for use in life tables and the calculation of r_s.

Thirdly, when the skulls from each sex were classified into three age (since death) classes, no significant difference could be detected between the sex ratios of these classes and it could be concluded that in spite of a distortion in the sex ratio of live wildebeest, the sexes were still killed by lions in the same ratio. Therefore it is unlikely that sex-specific predation had occurred which could have contributed to the decline in the proportion of adult cows to bulls discussed in the previous chapter. This lends further support to the considerable evidence given already that it was a distortion (favouring males) in one or more calf cohorts' initial sex ratio which led to the increase in the proportion of bulls in the population. Such a distortion in foetal sex ratios has been found in buffalo from the KNP (Whyte, Pienaar & Vos, 1984) though in that case the distortion favoured females.

Thus it seems that distorted foetal sex ratios may be one of an ungulate population's normal responses to changing environmental conditions which leaves the question: Can an ungulate population ever be considered to have a truly stationary age distribution?

5.4.3 Condition of wildebeest killed by lions

Unfortunately sample sizes of condition estimates of wildebeest killed by lions and of those shot at random were too small to detect any significant differences. Thus it could not be concluded that wildebeest killed by lions were in poorer condition than those who had escaped predation. Those killed by lions showed a wide variation in condition and therefore wildebeest in all degrees of condition are taken. However, the condition of bulls killed in summer was significantly better than those killed in winter, but as all wildebeest can be expected to be in poorer condition in winter, nothing more can be concluded. Larger samples over a greater number of winter and summer seasons are required to clarify this aspect of the lion-wildebeest relationship.

5.4.4. Radio telemetry

This aspect of the study proved somewhat disappointing in that the data on the species composition of prey killed by lions and the age/sex structure of the sample of wildebeest kills were too small for satisfactory analyses or extrapolation to the whole wildebeest population of the CD. No seasonal differences could be detected in the species composition of prey in the lions' diet. The influx of migratory wildebeest into the study area in summer was expected to result in an increased proportion of this species killed by lions but the data could not confirm this. Also, as territorial bulls remain on their territories in winter and do not follow the migration, it was expected that in winter a higher proportion of bulls would be killed than cows but this could also not be proven. In both cases the inability to draw significant conclusions was probably due to the limitations of the data - especially the small sample sizes. However, data on pride sizes and home ranges proved more useful and from this study and from that of Smuts (1978a) results suggest that neither of these variables have changed and that the lion population of at least the Sweni/Mlondozi area is stable or has remained stable since 1976. As this area is relatively homogeneous in terms of wildebeest habitat, it was felt that there was reasonable justification for extrapolating the data from the 10 radio-collared prides to the other nine in this area in an attempt to assess the impact of lions on this sub-population.

From the basic assumptions (a) that the number of prides and their respective sizes had not changed, (b) that the estimated mean frequency at which these prides kill is correct, (c) that the proportion of wildebeest in all 19 prides' diet during respective years was the same as for the 10 study prides, (d) that the mean proportion of adult wildebeest cows obtained from ground counts was accurate, and (e) that the 80% pregnancy rate given for adult cows by Braack (1973) still held for this study period, it was calculated that lions could have removed up to as much as 85,6% of the estimated recruitment to the wildebeest population in one year. Clearly, if these assumptions are valid, lions possess a considerable potential to limit this wildebeest sub-population's growth.

Other studies have shown that predators are capable of limiting or reducing prey populations. Hirst (1969) concluded that lions were limiting the wildebeest population of the Timbavati Private Nature Reserve which borders on the CD's western boundary, and Mech & Karns (1977) concluded that although adverse habitat factors were the indirect causes of a decline in a white-tailed deer population, increased predation by wolves was the ultimate mortality factor.

Thus, although based on samples which may have been too small to be statistically significant, the tentative conclusion must be that lions, as in the case of wolves with white tailed deer, are the ultimate mortality factors which are indeed capable of limiting and even reducing the wildebeest population of the CD during periods when habitat conditions are sub-optimal and provide indirect stimuli for a population decline.

The high proportion of buffalo in this kill sample confirms the switch in prey from wildebeest which was indicated by the preference ratings calculated from Rangers' returns. The subsequent decline in the buffalo population of the CD which was in excess of the number culled, suggests that lions may also be capable of reducing this species' population should environmental and/or habitat changes be unfavourable. Waterbuck have also consistently produced high preference ratings and this study has shown that vulnerability shifts occur between wildebeest and waterbuck - indications that lions are also limiting on this population. The zebra population of the CD also declined and then recovered in a similar fashion to the wildebeest population between 1970 and 1984 (Joubert, 1978 - 1982; 1983c; 1984; Joubert, Pienaar, van Wyk & Smuts, 1974; Smuts, 1975b; 1976b; 1978b; 1978c) largely for the same reasons as for wildebeest and therefore lions may have the potential to limit this population as well. Hirst (1969) also found that an increase in giraffe kills to be correlated to a decrease in wildebeest kills in the Timbavati Private Nature Reserve.

Therefore, if lions are capable of limiting these populations, it is not inconceivable that they may also have the potential to limit some if not all of the other major species in their prey spectrum.

A final conclusion for this section is that future predator-prey studies to be conducted in a similar fashion to this one, where a limited number of workers are to collect information from a limited number of predators with the objective of extrapolating the results to large predator and prey populations should be very carefully considered. The extensive assumptions which unavoidably have to be made are too tenuous to allow a convincing conclusion which would require a far greater input in terms of manpower and time to obtain larger samples from larger numbers of predators, their kills, and their prey species' populations.

5.4.5 Effects of predator culling

Two parameters were available for an assessment of the effect of predator culling on the wildebeest population. Predator culling was conducted in the Sweni/Lindanda area and thus would affect only the wildebeest of the Sweni/Mlondozi sub-population while the Satara sub-population was available as a control. These two parameters were calf survival rates and sub-population growth rates. Initially higher calf survival rates in the Sweni/Mlondozi sub-population suggested that the predator cropping was achieving its objective but as this sub-population migrated out of the Sweni/Lindanda area in winter and were thus exposed to normal predator pressure during that time, the advantage had been lost before the calves had reached two years old.

The two sub-population's growth rates also showed no significant response to the removal of lions and hyaenas and followed an almost identical trend over the period.

Thus, in terms of both calf survival and sub-population growth rates, it can be concluded that the predator culling, as it was practised in only part of the migratory wildebeests' range, was not achieving its objectives. Predator culling over the whole of this sub-population's range would involve the removal of a far greater number of these two predators - an option that was obviously unacceptable and, as both sub-populations had by then begun to show an increasing trend, predator culling was terminated.

CHAPTER 6
GENERAL CONCLUSIONS

While the more specific conclusions that were drawn from results of each aspect of the study were given at the end of each relevant chapter, the more general conclusions are given here in terms of the stated objectives of the study (see section 1.3)

6.1 MOVEMENT PATTERNS AND SUB-POPULATIONS

Though Pienaar (1960) was the first to outline the movements of the Western Boundary sub-population, it was Smuts (1972) who initially showed that there were three separate sub-populations in the CD from his observations on the movements of marked zebra. Braack (1973) concluded that the same sub-population boundaries existed for the wildebeest population, but the upheaval caused in the Western Boundary sub-population by the western boundary fences severing its migration routes and excising its summer grazing grounds, suggested that the sub-populations' movement patterns and boundaries may have changed.

Observations on the 87 wildebeest marked during this study showed that the sub-population boundaries indicated by the above authors had not altered significantly and that crossing of these boundaries by wildebeest was minimal. This validated the separate analysis and comparison of the respective sub-populations' growth and structural characteristics and sub-population boundaries were defined which conformed to the grid system utilized for computerised data storage of the ecological aerial survey data. These exact boundaries are shown in

Figure 4.1.1 and given in Appendix B. One of the major differences between the findings of this study and those of Pienaar (1960) and Braack (1973) was that the Western Boundary sub-population is no longer migratory. Wildebeest in this sub-population are now confined to isolated "islands" of suitable habitats in the *Acacia* veld on Gabbro landscape and on the ecotones or "seeplines" in the Mixed *Combretum/Terminalia sericea* Woodland landscape. No significant movement was recorded in this sub-population which must now be considered as sedentary and not migratory as in the past. The other two sub-populations' statuses are still as they were described by Braack (1973). This for the Satara sub-population is that they are largely sedentary showing no regular seasonal migrations though they may undertake fairly extensive movements to utilize optimal conditions created by fire etc. The Sweni/Mlondozi sub-population is still migratory, spending winters in the south of their range around Mlondozi and summers in the north in the Sweni/Lindanda area. Although very few wildebeest remain in the Mlondozi area in summer there is apparently a sedentary element which over-winters in the Sweni/Lindanda area, and many territorial bulls do so as well.

6.2 RECENT HISTORY OF THE THREE POPULATIONS

Confirmation of the validity of separately analysing sub-population data made it possible to trace the trends of the sub-populations since 1978 when ecological aerial surveys were initiated in the CD. This unfortunately was just before the nadir of the population decline so previous data were not available, Pienaar (1965) however, gave population totals and distributional data of the wildebeest recorded during the first comprehensive aerial census. These data could therefore also be allocated to the relevant sub-populations and proved vital in illuminating the causes of the decline.

Between 1965 and 1979 the population of the CD declined from 12 197 to 4 768 (a decline of 61%). During the same time the Western Boundary sub-population declined from 5 914 to 752 (87%), the Satara sub-population from 3 149 to 2 012 (36%) and the Sweni/Mlondozi sub-population from 3 134 to 2 004 (36%). Thus the decline in the Western Boundary sub-population by far exceeded those in the other two sub-populations and their respective contributions to the total decline were Western Boundary - 69,5%, Satara - 15,32% and Sweni/Mlondozi - 15,2%. The almost identical declines and subsequent recoveries of the Satara and Sweni/Mlondozi sub-populations was in complete contrast to the total crash of the Western Boundary sub-population which up until the time of writing has shown little sign of a recovery, and it is clear that factors affecting the former two sub-populations were not the same as those affecting the latter. The only possible factor which could have acted on this, the largest sub-population, and not on the other two was the severing of its migration routes, the excision of its summer grazing grounds and in fact the total disruption of its ecological foundation by the erection of first the western boundary fence in 1961 to retain them within the sanctuary, and then the secondary fence* from the Albatross corner to the one at Adger (Figure 3.1.1) in 1966, which was to prevent the wildebeest and zebra from over-utilising this area of prime habitat.

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* It has not been the intention anywhere in this thesis to in any way incriminate those who had either of these two fences erected, as I believe the decisions made were unquestionably considered to be in the best interests of nature conservation at that time. It is only now that we who have the advantage of hindsight can analyse and objectively interpret the effect that these fences had on the game populations.

These fences provided the indirect stimuli for the sub-population's decline but the ultimate mortality factors can now only be guessed at. Some direct mortality was caused by the fence itself (Anonymous, 1963) and predators also made some use of it to capture prey (Adendorff, 1984). However, the reduction in the size of this sub-population's range suitability as a wildebeest habitat, rendered it no longer capable of sustaining this large sub-population and in fact could not sustain its migratory elements at all and they gradually dwindled to the lowest recorded level of only 752 individuals in 1979. As was the case with the Satara and Sweni/Mlondozi sub-populations, the wet cycle may have played some role in this decline as subsequent to 1979, all three have shown an increase though it has been very modest in the Western Boundary sub-population.

The conclusions to be drawn are that the Satara and Sweni/Mlondozi sub-populations declined as a natural response to a change in habitat conditions which were induced by the above-average wet cycle, but recovered as the drier, more normal conditions returned. However, the decline in the Western Boundary sub-population was inevitable once the fence/s had been erected but it was probably accelerated by the wet cycle conditions. This sub-population has now attained a new but greatly reduced level which is in harmony with its prevailing habitat's ecological dictates and will in future probably fluctuate around this new level in accordance with prevailing climatic and habitat conditions. It is unlikely that elements in this sub-population will ever again undertake the seasonal migrations as they were known in the past.

6.3 SEX AND AGE STRUCTURE OF THE POPULATION

6.3.1 Adult sex ratio

Adult sex ratios and calf recruitment rates were monitored for six years using data gathered on ground counts. From 1978 onwards the adult sex ratio underwent a distortion which first favoured bulls until it reached a ratio of about 1 bull to 1,7 cows between 1980 and 1981. It then gradually returned to around what it had been when the counts were initiated of approximately 1 bull to 2,5 cows. All the evidence from data gathered during this project suggest that it was not an increased mortality rate in cows or an increased survival rate of bulls which induced this distortion and the only other means by which this sex ratio could have changed is due to an increasing recruitment of bulls to the adult segment of the population. For this to have occurred there must have been either an early higher mortality in female calves than in male calves or a distortion favouring males in foetal or natal sex ratios which persisted through to the adult segment of the population. Although it was found that male caribou (Rangifer tarandus) calves were more vulnerable to attack by lynxes on the island of Newfoundland (Bergerud, 1983) there was no evidence to suggest that a mortality factor was acting disproportionately on female wildebeest calves which could have later induced a bias in the adult sex ratio. On the other had there is a host of literature on variation in foetal sex ratios, much of which has been reviewed by Clutton-Brock and Albon (1982) and Verme (1983). Nutritional status of the mother was found to influence the sex ratio of their offspring in white tailed deer (Odocoileus virginiaunus). Mothers on a low plane of nutrition produced offspring at a natal sex ratio of 0,43 females per male while those maintained on a high nutritional plane produced calves at 1,14 females per male (Verme, 1983). Whyte, (in prep. b) however, found the reverse to be true for buffalo in the KNP and cows stressed by continuing drought conditions and thus on a low level of nutrition had a significantly skewed foetal sex ratio of 1,68 females per male while for those not subjected to nutritional stress the ratio was 0,92 females per male. In buffalo therefore, drought conditions induce an increase in females born to the population while under mesic or favourable conditions the reverse is probably true.

If in fact the distortion in the adult sex ratio of the wildebeest population was caused by one or more calf cohorts with skewed natal sex ratios entering the adult segment, this conforms to the response in buffalo as the greater number of bulls born to the population would have been conceived during the wet cycle when the cows were on a high level of nutrition.

The adaptive modification of progeny sex ratios was discussed by Clutton-Brock & Albon (1982). They concluded that if modification was possible, there was no reason why selection should not exploit this potential. The physiological mechanisms which ultimately determine the sex of the offspring are as yet poorly understood but are probably related to differences in motility of X- and Y-bearing spermatozoa which could be dependent on physiological determinants in the parents (Clutton-Brock & Albon, 1982).

Whatever the adaptive significance to the parents may be of producing male or female offspring under different environmental conditions, the response shown by buffalo and probably also wildebeest, would appear to hold some clear advantages as a self-regulating mechanism to the population as a whole. If a population had undergone a decline due to a period of severe drought, more female offspring would increase its reproductive potential so as to optimise on improved conditions as and when they came. A few bulls could serve many cows so a smaller proportion of bulls would not interfere with the reproductive success of the population as a whole. Maternal investment in rearing female offspring to weaning is less than in male offspring which would enhance the chances of survival of both mother and female calf (Clutton-Brock & Albon, 1982). If on the other hand, a population increasing under optimal conditions produced more male young, this would tend to retard population growth while prevailing conditions favoured highest survival rates. More bulls in the population would also increase competition for the higher ranks in the social hierarchy ensuring that only the dominant (fittest) bulls would serve the smaller proportion of cows. Wet and dry periods in the climatic cycle of the sub-continent are in the region of 10 years (Tyson and Dyer, 1978; Gertenbach, 1980) which is well in excess of the maturation time of wildebeest and buffalo which would allow enough time for these skewed foetal sex ratios to respond to the prevailing climatic cycle to the advantage of the population. Such increased or decreased population growth rates would counteract excessive and possibly dangerous population fluctuations. But, if this theory is valid, why then were more bulls being produced (suppressing population growth) when the population was actually in a state of decline? The answer to this is probably that the high nutritional plane of the animals was inducing a foetal sex ratio distorted in favour of males, but it was the rank habitat conditions and vulnerability to predators that was causing the decline. The 1970-1979 wet cycle was by far the wettest ever recorded for the KNP and it is possible that such a strategy, which may function normally under more average wet cycles, could not adjust to the abnormally wet conditions which prevailed between 1974 and 1978. This was just the time when these "excess" bulls would have been conceived and born.

6.3.2 Cow/calf and cow/yearling ratios

Between January 1978 and January 1984 the cow/calf (first year of life) and cow/yearling (second year of life) ratios of six calf cohorts was monitored from birth to 21 months old. One other, born in 1977 was monitored only for its second year, one born in 1983, for only its first year while for the January 1984 calf cohort only one count just after birth was conducted. It was hoped that these ratios might prove useful as predictors of population trend but from ground count data, calf mortality can at best only be expressed as a proportion of the adult cows. Adult female mortality however, cannot be measured from this data. For example, if for some reason adult female mortality during a particular year was high, all those females' calves of less than a year old would almost certainly also die. The measured cow/calf ratio may then still be high suggesting a large increase in the population though the actual increase may be very small. For this probable reason the cow/calf ratios did not correlate well with population trends.

A point to be considered when cow/calf ratios are to be compared is that these ratios were found to decline sharply after birth and were therefore heavily dependent on the time that had elapsed between birth and the count. Thus only data collected at similar time spans after the birth peak are comparable.

Considerable variation was also found to occur between respective cohorts' cow/calf and cow/yearling ratios at similar times of year. At one year old, there was a variation of between 24,0 and 60,1 calves per 100 cows while at 21 months old the range was from 20,6 to 34,3 yearlings per 100 cows. This represents a significant variation in the recruitment to the population for respective years.

The ground count data gathered over this six-year period suggest that the adult sex ratio is not stable and that calf and yearling mortality is highly variable. If a distortion in the adult sex ratio of this population is an unusual event, it seems unlikely (though not impossible) that this study should have been initiated right at the beginning of such an event and have ended at its termination. It seems more likely that the sex ratio varies around a central mean and the distortion observed during this study was just one of its normal fluctuations. If so, and as recruitment rates are also highly variable, could a population such as this ever be considered to have a stable age and/or sex distribution?

6.4 IMPACT OF LIONS

This aspect of the study was comprehensively covered in the previous chapter and to avoid duplication the reader is referred to Section 5.3.4.5. However, some theorising remains to be done. In the light of evidence presented in this thesis, particularly with regard to the potential impact of lions not only on the wildebeest population but on the other major prey species as well, the delicate shifts in vulnerability and the switching of prey in accordance with the dictates of the habitat, and the population fluctuations which must be regarded as a normal function in these populations, I propose the following summary of the dynamics of the predator/prey/habitat relationships in a large Lowveld ecosystem. Each of the major prey species of lions in the ecosystem has evolved to a specialised habitat niche all of which are available in the ecosystem to a greater or lesser degree. The size of each of these habitat niches ultimately determines the size of the specific populations that have evolved to utilize them. Given optimum habitat conditions any population will increase even in the presence of a broad spectrum of predators, but these habitats are not stable either spatially or temporally in an optimum condition - they may become more or less favourable through physiognomic changes in the vegetation (Coetzee, Gertenbach & Nel, 1977) or a host of other habitat factors which probably all undergo changes according to the prevailing climatic cycles which have been shown to occur. Other factors such as fire may also dictate the condition of the habitat but the frequency of natural fires has also been shown to be related to climatic cycles (Gertenbach, 1980b). The condition of each prey species' habitat is therefore ultimately determined by the prevailing climatic cycle which will in turn determine the vulnerability of that species to its predators. Optimum habitat condition for one species may not be or will not be optimum for another. This was shown to be the case from census figures during the wet cycle of the 1970's when the zebra and wildebeest declined due to the rank conditions but all other major herbivore species increased (buffalo, waterbuck, kudu, giraffe, warthog, impala). Each species, therefore, has an inherent resistance to predators under optimum habitat conditions which decreases as the suitability of the habitat deteriorates. This facilitates prey switching in the lions of the area from a species that was previously vulnerable to one whose vulnerability is increasing. Thus, owing to a wide spectrum of available prey species whose vulnerability is dependant on its specific habitat requirements in a dynamic mosaic of habitat types which are constantly undergoing physiognomic and other changes in accordance to prevailing climatic conditions, lions constantly have access to one or more prey species that they are able to exploit due to an increase in vulnerability. This means that lions are able to maintain a relatively stable population while their prey species fluctuate. The picture presented here is simplified as other mortality factors have been ignored. These include other predators and though these other predators may not have the same potential to reduce a population of a prey species, vulnerability and prey switching will also largely determine the relative proportion of each species in its diet. Another important mortality factor is drought. Under extreme conditions drought can induce population declines due to malnutrition in excess of the capabilities of predators as was the case in 1982/83 in impala, kudu, warthog, buffalo and others in the CD and elsewhere in the KNP (Joubert, 1983c). Less severe droughts, however, may only induce habitat change and a deterioration in physical condition among some species which will render them more vulnerable to predation.

Climatic cycles are therefore probably essential in maintaining diversity in an ecosystem such as the CD. A uniform climatic regime whether it were wet or dry would induce the vegetation towards a climax determined by the regime and could ultimately result in the extirpation of species favouring the opposite climatic conditions. Fluctuating climatic cycles favour first one species then another creating conditions which allow the co-existence of species favouring either relatively mesic or arid conditions.

Population fluctuations should therefore not be anticipated with trepidation but should be considered to be natural phenomena which in fact are essential for the maintenance of species and habitat diversity, and although the major decline in the wildebeest population was induced in the Western Boundary sub-population by the boundary fence, the other two sub-populations underwent natural declines in the age-old pattern. The former gives cause for disappointment - the latter should be viewed with the wonder accorded to most other natural processes.

CHAPTER 7

MANAGEMENT CONSIDERATIONS

The management proposals which are given below are based on four considerations. These are:

a) Population maxima of 12 000 and minima of 8 000 had been set for both the wildebeest and zebra populations of the CD (Joubert, Pienaar, van Wyk & Smuts, 1974). During the respective declines in these populations, both dropped below the minimum levels set and culling was terminated but this did not end the decline which in wildebeest was eventually to reduce the population to around 4 500. Smuts (1975b) felt that the culling of this population just as it began its own natural decline may have accelerated and magnified the crash - inducing the nadir to a lower level than would have been the case in the absence of culling. This contention has never been satisfactorily proved or disproved, and not enough is known about the natural ceilings these populations will reach or to what extent natural declines will reduce them in the absence of culling.

b) Bell (1971) found that in the Serengeti a natural grazing succession occurred. Buffalo initially entered a long grass area and through grazing and trampling modified the structure which rendered it more suitable to zebra who by the same means modified it further. Wildebeest were then attracted and they moved in in large numbers which resulted in heavy utilization by them. Through reduced competition with dominant grasses, forbs made their appearance in the field layer which attracted the gazelles (*Gazella* spp.) - the last of the species participating in this grazing succession. There is some evidence (own observations) that a similar succession may on occasions also operate in the CD, and Smuts (1976b) felt that buffalo could play a significant role in habitat modification which during the wet cycle could have alleviated the pressure caused by the rank conditions on the zebra and wildebeest populations but the culling of these three species has obscured much of the understanding of the grazing inter-relationships between them which could have been gained during the wet cycle declines.

c) From the data gathered and analysed during this study, it was shown that subtle shifts in vulnerability to lions occur according to prevailing conditions. Lions also were shown to switch from one prey species to another according to vulnerability which could result in the relief of predator pressure on the one and possibly induce a decline in the other (as was probably the case in the switch from wildebeest to buffalo). However, enough is not yet known about these shifts between prey species or in predator vulnerability. If buffalo culling had not been practised in the CD, it is possible that due to their greater abundance - and therefore availability - the switch to buffalo may have happened sooner and the decline of the wildebeest may not have been as severe.

d) Modern ecological aerial surveys have been developed and refined to a highly reliable and repeatable technique which allows the sensitive monitoring of population trends. Many environmental parameters are also monitored which can be correlated to these trends and thus the responses of these populations to environmental stimuli can be gauged.

In the light of these four considerations I propose:

1) That the population ceilings set for wildebeest and zebra be ignored in future so as to allow these two species to attain their own natural ceilings of which we are as yet, still unsure, and to afford them the opportunity of undergoing their natural fluctuations in accordance with climatic and environmental changes.

2) That for the same reasons as for zebra and wildebeest above, buffalo culling in the CD be terminated and the population allowed to attain its natural ceiling.

3) That the responses of these three populations (and indeed the populations of the other major species) be monitored as is done at present through ecological aerial surveys and that by the same means, habitat factors also be monitored.

4) That predator-prey relationships continue to be monitored by the calculation of annual preference ratings from data in Rangers' returns.

Little is known of the inter-relationships between the major grazing ungulates in the KNP. I believe that once the wildebeest, zebra and buffalo populations have begun to fluctuate naturally in the absence of population control (culling), sensitive monitoring of these populations and their relationships with their predators and their environment will begin to provide real insights on an increasing scale into the functioning of this complex ecosystem.

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APPENDIX A

TABLE OF THE DOMINANT AND CHARACTERISTIC PLANT SPECIES OCCURRING IN THE LANDSCAPES OF THE CENTRAL DISTRICT OF THE KRUGER NATIONAL PARK*

SPECIES	LANDSCAPE WHERE RECORDED (see key below)																
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
WOODY SPECIES																	
Acacia borleae			X						X						X		
Acacia burkei						X						X				X	
Acacia caffra																X	
Acacia exuvialis	X	X	X	X		X	X	X				X			X	X	X
Acacia gerrardii						X						X	X		X	X	
Acacia grandicornuta																	X
Acacia nigrescens	X	X	X	X		X	X	X	X	X	X	X	X	X	X		X
Acacia nilotica	X														X		X
Acacia robusta				X		X						X			X		X
Acacia senegal var. *leiorhachis*				X													
Acacia tortilis		X	X	X			X	X	X		X	X	X	X	X		X
Acacia welwitschii subsp. *delagoensis*													X	X			
Acacia xanthophloea		X		X											X		
Acokanthera oppositifolia				X													
Adansonia digitata			X		X												
Adenia spinosa					X												
Adenium obesum																	X
Afzelia quanzensis										X						X	

* Summarised from Gertenbach (1983a) ■ Landscapes favoured by wildebeest

KEY

1. Olifants River Rugged Veld
2. *Colophospermum mopane* Shrubveld on Basalt
3. *Combretum/Colophospermum* Rugged Veld
4. *Combretum/Acacia* Rugged Veld
5. Lebombo North
6. *Combretum/Colophospermum* Woodland of Timbavati
7. *Colophospermum mopane* Shrubveld on Gabbro
8. Bangu Rugged Veld
9. Dwarf *Acacia nigrescens* Savanna
10. Pumbe Sandveld
11. *Acacia* on Gabbro
12. Mixed *Combretum/Terminalia sericea* Woodland.
13. *Acacia welwitschii* Thickets on Karoo Sediments
14. Kumana Sandveld
15. *Sclerocarya birrea/Acacia nigrescens* Savanna
16. Lebombo South
17. Thickets of the Sabie River

SPECIES	LANDSCAPE WHERE RECORDED																
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
Albizia anthelmintica	X																
Albizia brevifolia	X															X	
Albizia forbesii														X			
Albizia harveyi	X	X	X			X	X				X	X		X	X	X	
Albizia petersiana subsp. *evansii*													X				
Androstachys johnsonii					X												
Anthocleista grandiflora																	X
Azima tetracantha									X								
Balanites maughamii														X			X
Berchemia discolor				X			X										X
Berchemia zeyheri																X	
Bolusanthus speciosus						X					X	X	X				
Boscia albitrunca	X		X	X	X											X	
Boscia mossambicensis									X				X				
Breonadia microcephala				X													X
Bridelia cathartica														X			
Bridelia micrantha	X																
Bridelia mollis							X										
Cadaba natalensis									X								
Capparis tomentosa				X	X				X				X				
Cassia abbreviata					X		X			X				X		X	
Cassine aethiopica												X					
Cissus cordifolia	X		X			X	X					X			X		
Cissus rotundifolia					X												
Colophospermum mopane	X	X	X			X	X										
Combretum apiculatum	X	X	X	X	X	X	X			X	X	X		X	X	X	X
Combretum collinum subsp. *gazense*										X							
Combretum erythrophyllum																	X
Combretum hereroense	X	X		X		X					X	X		X	X		X
Combretum imberbe	X	X	X	X		X						X			X		
Combretum molle										X							
Combretum mossambicense		X	X	X	X		X										
Combretum zeyheri						X				X		X				X	

SPECIES	LANDSCAPE WHERE RECORDED																
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
Commiphora africana	X					X	X	X				X					
Commiphora glandulosa		X		X													
Commiphora mollis	X		X		X		X									X	
Cordia ovalis				X					X								
Cordia sinensis									X								
Croton gratissimus					X											X	X
Croton megalobotrys		X		X											X		
Dalbergia melanoxylon	X	X	X			X	X			X	X	X			X		
Dichrostachys cinerea subsp. africana	X	X	X	X		X	X	X	X	X		X	X	X	X	X	X
Diospyros mespiliformis				X		X	X					X		X	X		X
Diospyros usambarensis										X							
Dombeya cymosa																X	
Dombeya rotundifolia							X										
Ehretia rigida		X	X						X			X	X		X		X
Ekebergia capensis																	X
Elephantorrhiza burkei					X											X	
Erythrina humeana																X	
Erythroxylum emarginatum														X		X	
Euclea divinorum			X			X						X	X		X		X
Euclea natalensis						X								X			
Euclea undulata														X			
Eugenia zeyheri										X							
Euphorbia confinalis					X											X	
Euphorbia cooperi					X											X	
Euphorbia guerichiana		X															
Ficus ingens																X	
Ficus smutsii	X																
Ficus soldanella					X		X							X		X	X
Ficus sycomorus				X											X	X	X
Galpinia transvaalica				X												X	
Garcinia livingstonei	X																
Gardenia resiniflua					X		X										
Gardenia spatulifolia				X													X

SPECIES	LANDSCAPE WHERE RECORDED																
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
Grewia bicolor	X	X	X	X	X	X	X	X			X	X	X	X	X	X	X
Grewia flavescens	X				X		X							X		X	X
Grewia hexamita					X		X										X
Grewia monticola														X			
Grewia villosa	X	X						X									
Hexalobus monopetalus	X																
Hippocratea longipetiolata				X										X		X	
Holmskioldia tettensis	X																
Hymenodictyon parvifolium					X											X	
Hyphaene natalensis		X													X		
Iboza riparia																X	X
Kigelia africana															X		X
Kirkia acuminata		X		X	X		X									X	
Kirkia wilmsii	X																
Kraussia floribunda																X	
Lannea discolor																	X
Lannea schweinfurthii	X	X			X	X	X			X	X	X		X	X	X	X
Lonchocarpus capassa		X		X		X				X		X	X		X		X
Maclura africana																X	
Maerua machonica				X													
Maerua parvifolia	X	X	X	X		X		X	X				X		X		
Maerua rosmarinoides																X	
Manilkara mochisia			X	X										X		X	
Maytenus heterophylla	X											X		X	X		
Maytenus senegalensis				X										X	X		
Maytenus tenuispina																	X
Monodora junodii																X	
Newtonia hildebrandtii																X	
Nuxia oppositifolia																	X
Ochna natalitia																X	
Olax dissitiflora	X															X	
Ormocarpum trichocarpum			X			X			X		X	X			X		X
Ozoroa engleri	X	X								X					X	X	
Ozoroa paniculosa																	X

SPECIES	LANDSCAPE WHERE RECORDED																
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
Pappea capensis	X		X	X			X							X		X	
Pavetta catophylla																X	X
Peltophorum africanum												X		X			
Phyllanthus reticulatus					X									X			
Portulacaria afra																X	
Pouzolzia hypoleuca																X	
Pseudolachnostylis maprouneifolia										X							
Ptaeroxylon obliquum			X	X												X	X
Pterocarpus rotundifolius											X	X			X	X	X
Rhigozum zambesiacum	X		X														X
Rhus spinescens					X									X		X	
Salacia kraussii										X							
Salvadora angustifolia			X														
Schotia brachypetala				X		X						X		X			X
Sclerocarya birrea	X	X	X		X	X	X				X	X			X	X	X
Securinega virosa	X		X	X			X	X	X		X		X		X	X	
Sesamothamnus lugardii				X													
Spirostachys africana			X	X								X	X	X			X
Steganotaenia araliacea							X										
Sterculia rogersii		X		X			X									X	
Strychnos decussata					X											X	
Strychnos madagascariensis												X				X	
Teclea pilosa													X				
Tephrosia sericea										X						X	
Terminalia phanerophlebia																X	
Terminalia prunioides	X		X	X		X	X	X							X		X
Terminalia sericea						X				X		X					
Thilachium africanum														X		X	
Tricalysia allenii	X				X											X	X
Trichelia emetica				X											X		X
Vangueria infausta																X	
Vepris reflexa																X	

SPECIES	LANDSCAPE WHERE RECORDED																
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
Xanthocercis zambesiaca				X													X
Ximenia caffra					X	X								X	X		
Zanthoxylum humilis	X		X										X				X
Ziziphus mucronata	X					X	X		X		X	X		X	X		X
GRASSES																	
Andropogon gayanus												X				X	
Aristida argentea												X					
Aristida congesta subsp. *barbicollis*	X	X	X	X	X	X		X		X		X	X		X	X	X
Aristida congesta subsp. *congesta*	X	X															
Aristida curvata	X																
Bothriochloa radicans	X	X	X	X		X	X	X	X		X	X	X	X	X	X	X
Brachiaria eruciformes		X							X								
Brachiaria nigropedata										X		X				X	
Brachiaria serrata						X						X					
Brachiaria xantholeuca	X				X			X				X				X	
Cenchrus ciliaris		X	X			X			X		X						
Chloris gayana		X															
Chloris mossambicensis															X		
Chloris roxburghiana			X										X				
Chloris virgata											X		X		X		X
Cymbopogon plurinodis	X					X	X			X	X	X					X
Cymbosetaria sagittifolia					X												
Cynodon dactylon		X		X													
Dactyloctenium aegypteum													X		X		
Digitaria erianthia var. *pentzii*	X	X	X	X	X	X	X		X	X	X	X		X	X	X	X
Enneapogon cenchroides	X	X	X	X	X	X		X	X	X	X	X			X	X	
Enteropogon macrostachyus													X	X			
Enteropogon monostachyus	X																
Eragrostis gummiflua						X						X					
Eragrostis rigidior			X			X						X		X			X
Eragrostis superba		X	X			X	X			X	X	X		X	X		
Eragrostis trichophora																	X

SPECIES	LANDSCAPE WHERE RECORDED																
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
Fingerhutia africana	X	X	X	X			X										
Heteropogon contortus		X	X	X	X	X	X			X		X		X	X	X	X
Hyperthelia dissoluta												X					
Ischaemum brachyatherum		X							X								
Leptochloa uniflora		X															
Oropetium capense	X												X				
Panicum coloratum		X	X	X		X	X	X	X		X	X	X		X		
Panicum maximum	X	X	X	X	X	X	X		X	X	X	X	X	X	X	X	X
Perotis patens												X					
Pogonarthria squarrosa						X				X		X		X		X	X
Rhynchelytrum repens	X		X			X						X		X			X
Schizachyrium exile	X																
Schmidtia pappaphoroides		X	X	X		X	X	X	X	X	X	X		X	X	X	X
Schoenefeldia transiens															X		
Setaria woodii		X							X		X				X		
Sorghum versicolor		X							X								
Sporobolus consimilis		X							X								
Sporobolus fimbriatus		X	X									X		X	X		
Sporobolus nitens				X			X				X		X		X		X
Sporobolus panicoides	X																
Sporobolus smutsii				X					X				X		X		X
Themeda triandra		X	X	X		X	X		X		X	X		X	X	X	X
Tragus berteronianus	X		X										X				
Tricholaena monachne						X						X					
Trichoneura grandiglumis						X						X					
Urochloa brachyura			X									X					
Urochloa mosambicensis		X	X	X		X	X		X	X	X	X	X	X	X		X
FORBS																	
Abutilon austro-africanum	X					X					X		X				X
Abutilon guineense						X			X			X					
Abutilon ramosum						X										X	
Acalypha indica																X	
Achyranthes aspera	X					X							X			X	X
Agathisanthemum bojeri						X				X		X					X

SPECIES	LANDSCAPE WHERE RECORDED																
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
Aloe chabaudii																X	
Aloe sessiliflora																X	
Amaranthus thumbergii													X				
Aptosimum lineare										X							X
Asparagus falcatus														X		X	
Asparagus minutiflorus									X					X		X	
Asparagus plumosus	X		X			X						X					
Barleria affinis					X												
Barleria prionitis								X							X		
Bidens pilosa	X																
Blepharis integrifolia												X	X				X
Calostephane divaricata	X																
Cardiospermum halicacabum					X												
Cassia absus												X					
Cassia mimosoides		X										X			X		
Ceratotheca triloba			X									X					
Chascanum hederaceum															X		
Cienfuegosia hildebrandtii									X								
Cissus quadrangularis				X												X	
Cissus rotundifolia				X												X	
Clerodendrum ternatum		X	X									X					X
Commelina africana																X	
Commelina bengalensis	X						X					X	X			X	
Corbichoria decumbens							X										
Corchorus asplenifolius	X	X	X			X	X				X				X		
Corchorus trilocularis		X															
Crabbea velutina	X		X														
Crossandra mucronata																	X
Crotalaria virgulata												X			X		
Cucumis africanus												X					
Cyathula crispa									X				X				
Cyperus rupestris			X		X							X					
Cyperus sexangularis		X															
Cyphocarpa angustifolia	X		X			X					X	X	X				X

SPECIES	LANDSCAPE WHERE RECORDED																
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
Oicoma tomentosa		X	X														
Dioscorea sylvatica																X	
Dyschoriste rogersii			X			X											X
Epaltes gariepina												X					
Euphorbia neopolycnemoides			X			X	X										X
Evolvulus alsinoides						X						X					X
Fimbristylis complanata						X						X					
Gisekia africana													X				
Heliotropium steudneri	X	X	X	X	X		X	X		X	X		X		X		X
Hemizygia elliotii	X																
Hermannia boraginiflora												X					
Hermbstaedtia odorata															X		
Hibiscus micranthus	X		X	X		X						X				X	
Hibiscus palmatus													X				
Hibiscus pusillus							X										
Hibiscus sidiformes	X																
Indigofera bainesii			X			X	X										
Indigofera filipes										X		X					
Indigofera floribunda						X		X									
Indigofera heterotricha		X															
Indigofera schimperi		X															
Indigofera vicioides																X	
Ipomoea crassipes							X				X						
Ipomoea obscura		X					X								X		
Jatropha variifolia																X	
Justicia flava						X							X		X		X
Justicia kraussii	X																
Kalanchoe rotundifolia																X	
Kohautia virgata						X				X		X					X
Kyllinga alba																X	
Lantana rugosa				X							X						
Leucas glabrata			X									X					
Mariscus dregeanus																X	
Mariscus rehmannianus	X																
Melhania forbesii	X																
Melhania rehmannii	X		X	X													

SPECIES	LANDSCAPE WHERE RECORDED																
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
Merremia kentrocaulus		X															
Merremia tridentata												X					
Neuracanthus africanus		X		X					X				X				
Ocimum americanum	X												X				
Pavonia patens				X		X	X				X	X			X		
Phyllanthus asperulatus	X		X				X					X	X		X		
Phyllanthus pentandrus							X										
Pupalea lappacea						X							X			X	X
Rhinacanthus rotundifolius						X											
Rhyncosia densiflora															X		
Rhyncosia minima		X													X		
Rhyncosia totta		X	X	X		X	X					X					
Ruellia patula			X			X							X				
Sansivieria dessertii																X	
Sansivieria hyacinthoides	X		X	X					X					X		X	X
Sarcostemma viminale				X										X		X	
Seddera capense		X	X	X													
Seddera suffruticosa											X		X				
Selaginella dregei					X												
Senecio longiflorus													X				
Sericorema remotiflora		X	X												X		
Sesbania sesban		X															
Sida rhombifolia											X						
Solanum coccineum													X				
Solanum panduraeforme	X	X						X			X		X		X		
Stylosanthus fruticosa												X					
Sutera bolusii		X															
Tephrosia multijuga		X															
Tephrosia polystachya	X	X	X	X		X	X				X	X			X		X
Thunbergia dregeana			X														
Tragia dioica					X		X					X	X				
Typha latifolia		X															
Vernonia fastigiata		X				X	X										
Vernonia oligocephala															X		
Vigna triloba		X															
Waltheria indica	X					X						X					X
Xerophyta retinervis	X																

APPENDIX B

COMPUTER LIST OF SUB-POPULATION BOUNDARIES

For computer extraction of sub-population totals, each grid square is examined by moving along the rows from west to east, starting at row 40 and at the completion of each grid row, moving south to the next.

The computer reads each row as per the extract of the program below as follows: e.g. in the first (northern most) line of the grid the instruction reads: 3,2240A,2 which the computer interprets as "Move along grid row 40 totaling all wildebeest encountered until grid No. 2240A is reached. All totals in this row up to this grid fall in Sub-population 3 (Western Boundary). Subsequent to this all totals fall in Sub-population 2 (Satara). As a second example in row 26 the instruction reads 3,2028D,2,2328D,1,2728C,2 which the computer interprets as "From west to east along row 28 all wildebeest fall into Sub-population 3 up to and including grid 2028D, after which they fall into Sub-population 2 up to and including grid 2328D. Thereafter they fall into Sub-population 1 (Sweni/Mlondozi) up to and including grid 2728C whereafter all totals fall into Sub-population 2.

TYPE B:ASMAPGNU.DAT

```
6
3,2240A,2
3,2240C,2
3,2239A,2
3,2239C,2
3,2138A,2
3,2038D,2
3,2037B,2
3,1937D,2
3,1936B,2
```

3,1936D,2
3,1935B,2
3,1935D,2
3,1934B,2
3,1934D,2
3,1933B,2
3,2033D,2
3,2032B,2
3,2032D,2
3,2031B,2
3,2031D,2
3,2030B,2
3,2030D,2
3,2029B,2
3,2029D,2
3,2028B,2
3,2028D,2,2328D,1,2728C,2
3,2027B,2,2327A,1
3,2227C,1
3,2226A,1
3,2226C,1
3,2225A,1
3,2225C,1
3,2224A,1
3,2224C,1
3,2223A,1
3,2223C,1
3,2222A,1
3,2422C,1
3,2421A,1
3,2421C,1
3,2420A,1
3,2420C,1
3,2419A,1
3,2419C,1
3,2418A,1
3,2418C,1
3,2417A,1
3,2417C,1
3,2416A,1
3,2416C,1
3,2415A,1
3,2415C,1
3,2414A,1
3,2414C,1
3,2413A,1
3,2413C,1
3,2412A,1
3,2412C,1
3,2411A,1

Ukulinga species composition Treatment ___________ Rep ______ Plot
Date ___________________ Observers

Species				
Aristida junciformis				
Brachiaria serrata				
Cymbopogon excavatus				
Diheteropogon amplectens				
Elionurus muticus				
Eragrostis capensis				
Eragrostis curvula				
Eragrostis racemosa				
Heteropogon contortus				
Hyparrhenia hirta				
Microchloa caffra				
Melinis nerviglumis				
Panicum aequinerve				
Panicum maximum				
Setaria nigrirostris				
Setaria sphacelata				
Setaria palleda-fusca				
Sporobolus stapfianus				
Themeda triandra				
Tristachya leucothrix				
Schoenoxiphium sparteum				
Bulbostylis sp				
Sedge				
Aeschynomene micrantha				
Agathisanthemum chlorophyllum				
Albuca sp				
Aloe maculata				
Abildgaardia ovata				
Acalypha punctata				
Argyrolobium molle				
Argyrolobium stipulaceum				
Anthospermum				
Aster bakeranus				
Becium obovatum				
Berkheya setifera				
Berkheya umbellata				
Cephalaria pungens				
Chaetacanthus burchellii				
Cheilanthus viridis				
Chaemacrista plumose				
Commelina erecta				
Conyza chilensis				
Cynoglossum				
Conyza chilensis				
Conyza floribunda				
Crabbea hirsute				
Cyanotus speciosa				
Corchorus asplenifolia				