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CONSERVATION MANAGEMENT OF THE KRUGER NATIONAL PARK ELEPHANT POPULATION

by

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This thesis is dedicated to those who have meant most to me in my life:

Merle Whyte

Lorna, Steven, Timothy & Christopher Whitfield

Neil & Natasha Whyte

Bill and Molly Whyte

Bill and Shirley Retief

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ABSTRACT

Aspects of history, population dynamics, movement patterns and impacts of elephants *Loxodonta africana* on baobab *Adansonia digitata* trees were studied in Kruger National Park (KNP). Techniques of elephant contraception were reviewed and effects on behaviour were studied. Options for elephant population management were investigated through modelling.

Three sub-populations of baobabs had different size-class structures. This was thought to result from exposure to different densities of elephants both spatially and temporally. These differences were suggestive of low historical densities of elephants.

A literature review of the long-term history of the KNP elephant population until initiation of management also inferred low historical elephant densities. The recolonisation of the KNP by elephants subsequent to proclamation as a game reserve was documented.

The history of the elephant management era including fencing of KNP and the elephant management policy of the time is reviewed and documented. Aspects of the dynamics of the

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population were studied from data collected at censuses and culls. Changes in rates of increase could be related to fencing and its effect on immigration and emigration.

A study of movements of radio collared animals showed that adult cows have distinct home ranges which are variable in size. Cows showed a high degree of fidelity to their home ranges. Culls induced movements but not beyond home range boundaries. Boundaries of management zones for a new elephant management policy were defined on the basis of these findings.

An analysis of census data examined the consequences of culling for the dynamics of the population. A distinct pattern in the rates of increase in culled sub-populations emerged. Densities declined in the year immediately following a cull but increased to significantly higher levels the year thereafter. This brought into question the effectiveness of culls in reducing elephant numbers in specific areas and the consequences for biodiversity. Changes in rates of increase may have resulted from intra-population movements rather than changes in demographic variables.

An overview is given of the broader issues of managing elephants and their local and global dilemmas. The logistics of implementing a contraception program were modeled showing that 75% of breeding cows must be under treatment to effect a stabilization of the population. A numerically simpler means of limiting population growth was identified. The killing or sterilization of 250 pre-breeding cows would achieve the same goal.

The new elephant management policy for KNP is documented. Expected population trends subsequent to the implementation of this policy are modelled. A personal evaluation of the policy is given.

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DISCLAIMER

This thesis consolidates into one document the results of research on the African elephant conducted by me and various respective co-workers. It was compiled from various published scientific papers and reports which were reworked into thesis format, but as a result, styles may vary between chapters. I testify that, except where otherwise acknowledged, the work in this thesis is my own, though it benefited from comments by my supervisor, co-authors, colleagues and referees.



I.J. Whyte

Skukuza, February 2001.

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CHAPTER 1: GENERAL INTRODUCTION

SCOPE OF THE STUDY

This thesis consolidates into one document the results of much of the research on the African elephant *Loxodonta africana africana* (Blumenbach 1797) population of Kruger National Park (KNP) conducted by me and various respective co-workers over the last decade. This has entailed a literature survey investigating the history of the population and an interpretation of the findings. It has also involved research into the impacts that elephant have had on the baobab *Adansonia digitata* population of KNP, and into impacts that management actions (such as culling and contraception) have had on the elephants, both at an individual level (through movement studies) and at the population level (through census data and data from culled animals).

The elephant population of the area now known as the KNP has undergone four distinct eras in the period of its history spanning the past 300 years or so. Each of these eras has received some attention as a separate chapter of this thesis, either through literature surveys or through research conducted by me independently or in collaboration with other co-authors. The thesis covers most of the important issues which the KNP population has undergone during this time, and in a sense it represents a history of the population.

The first of these eras ("the pre-management era") encompasses the period up to the time that managers perceived it necessary to limit elephant numbers in KNP. This era could perhaps have been divided into smaller periods as it includes the time before the arrival of Europeans, a period after their arrival when hunting decimated the population, and the time thereafter when the area had been proclaimed as a game reserve. But little information is available on some of these periods and it seemed more logical to lump them into one "pre-management era".

Before the arrival of Europeans, movements of elephants would have been largely unrestricted and the impact of humans on the population is not known, but some clues to their status during this era come from baobabs (due to their extreme longevity), from the paintings of the San people (Bushmen) and from a few other archaeological sources. The

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evidence presented here suggests that elephant densities during these times were always low but the reasons for this are obscure. This conclusion is a personal interpretation which may be somewhat controversial, as it does not concur with that of earlier authors (e.g. Pienaar 1990; Rowland-Jones1955). Human impacts could have been responsible for low densities, as computer modelling of the population dynamics (Whyte *et al.* 1998; see Chapter 6) suggests that an elephant population's growth can be checked by the selective removal of as little as 3% of the population per year. However, once the Europeans arrived with their guns, the population underwent a steep decline to the point of virtual extirpation, at which time the area was proclaimed a game reserve. This allowed re-colonisation by elephants and unrestricted population growth. This era ended once these two processes resulted in a perceived necessity for fencing the Park's boundaries and population limitation through culling.

"The management era" was the second of these eras and lasted while movements and population growth were actively limited through fencing and culling (including translocation) campaigns. The policy during this time was to maintain the number of elephants in KNP at around 7 000 (Joubert 1986). Aspects which receive attention in this thesis include population dynamics, a movement study, and an analysis of the impact of culling on sub-population dynamics.

Culling was suspended in 1995 due to an animal rights group who challenged the rights of South African National Parks (SANP) to kill elephant. SANP agreed to review their elephant management policy and placed a moratorium on culling until this review had been concluded. This review is now complete (Whyte *et al.* 1997; Whyte *et al.* 1999), but it still awaits final authority for its implementation. Subsequent to the moratorium, a "post-management era" has prevailed. This era has been characterised by SANP developing the capacity and equipment to move elephant family units and even the largest of bulls, and by research into contraception which was encouraged by SANP in the hope that it would provide an additional, ethically acceptable tool for the management of elephants.

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The final era represents a look into the future and is mainly comprised of the new policy for the management of the elephants of KNP (Whyte *et al.* 1997; Whyte *et al.* 1999). This policy heralds a new approach to the elephant management dilemma. As with the earlier policy (Joubert 1986) its primary objective remains the maintenance of KNP's biodiversity, but it will allow unrestricted population growth in some areas, while actively reducing numbers in others. The policy was compiled through a process which encouraged considerable participation from experts outside of SANP, and also from other "interested and affected parties".

OBJECTIVES OF THE STUDY

The main objective of the thesis has been to bring together the published and unpublished results of management related research conducted by me and various respective co-workers. The various subjects covered collectively present a history of the population, but each subject has its own specific objectives.

Chapter 3 presents the results of an investigation into the baobab population (Whyte, Nel, Steyn & Whyte 1996). The objectives were to:

- Document the structure of the various sub-populations of KNP's baobabs;
- Investigate differences in these sub-populations to assess elephant impacts;
- Look for possible clues to historical elephant densities from population structure data and old scars caused by elephant utilization.

Chapter 4 covers the "pre-management era" from results of a literature survey. Objectives were to:

- Document the known history from information gained from the survey;
- Provide an interpretation of possible historical elephant densities and/or trends from this information;

Chapter 5 is a compilation of published papers (van Aarde *et al.*1999; Whyte 1993) and hitherto unpublished research covering aspects of the management of the elephant

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population. Management aspects which receive attention are census and culling methods, population dynamics, and movements and home ranges. The objectives were to:

- Review and document census and culling techniques, and numbers of elephants removed from the population;
- Calculate estimates of the major determinants of the population's performance – sex ratios, pubertal age, calving interval, and from these, the rates of increase and mortality;
- Determine how sub-population rates of increase responded to culls;
- Determine clan home ranges and how movements of radio-collared individuals responded to culls.

Chapter 6 focuses on the post-culling era which was characterised by research into contraception of elephants. Two papers have been incorporated into this chapter (Whyte *et al.*1998; Whyte & Grobler 1997). Objectives were to:

- Model the dynamics and logistics of a contraception program to limit an elephant population;
- Use the model to identify a sex and age class in the population which would limit the culling to the least number of animals;
- Review the contraception research techniques as prospective means of managing the population;
- Assess the respective contraception techniques' effects on the behaviour of treated animals.

Chapter 7 presents and reviews the new management policy for the elephant population of KNP (Whyte *et al.* 1997; Whyte *et al.* 1999). The objectives were to:

- Document the process through which the policy was formulated;
- Present the policy;
- Give a personal evaluation of the new policy.

Finally, Appendix 1 presents a device developed for the estimation of birth and conception dates from foetal mass and date of collection (Whyte 1986).

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OTHER ELEPHANT RESEARCH IN KRUGER NATIONAL PARK

Although the management of elephants in KNP has attracted a considerable volume of media and other interest, relatively little research has been conducted on this aspect. Much effort has been put into censusing the population since 1967 as annual culling quotas were based on census results. These results have remained confined to internal (SANP) reports (see Chapter 5). Only one study on the dynamics of the population has been published (Smuts 1975) and a later study examined the impacts of culling on sub-population dynamics (van Aarde *et al.* 1999).

A long-term study of elephant home ranges has been underway since 1989 and receives some attention in this thesis (Whyte 1993; see Chapter 5). A cursory examination of the effects of culls on movements of radio-collared animals is included.

Other workers have focussed on the impacts that elephants have had on vegetation. These include the original work on which the acceptable upper limits of the elephant population were based (Pienaar *et al.* 1966; van Wyk & Fairall 1969). From data gained from aerial photographs, Viljoen (1988) noted a decline in mature trees which he attributed to elephants. Trollope *et al.* (1998) also examined long-term changes in the woody vegetation with reference to the effects of fire and elephants. Impacts on particular tree species were conducted on marula *Sclerocarya birrea* (Coetzee *et al.* 1979) and knobthorn *Acacia nigrescens* (Engelbrecht 1979). Two more recent studies have also focussed on baobabs *Adansonia digitata* and star chestnut *Sterculia rogersii* (Kelly 2000), and marula (Jacobs 2000).

Two studies of contraception in elephants have been conducted. The first used subcutaneous oestradiol-17ß implants. This project was terminated due to behavioural aberrancies (Whyte & Grobler 1997; see Chapter 6) and the results have not been published. The other used porcine zona pellucida immuno-contraceptive vaccine (pZP) and had some successes (Fayrer-Hosken *et al.* 2000; Whyte & Grobler 1997). An evaluation of these as a management tool was made by Whyte *et al.* (1998).

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Endocrinological studies have been conducted mainly from material collected at culls (de Villiers *et al.* 1989; Hodges *et al.* 1994; Hodges *et al.* 1997; McNeilly *et al.* 1983; Greyling *et al.* 1997; Greyling *et al.* 1998). The phenomenon of "musth" in elephant bulls has also been investigated (Hall-Martin & van der Walt 1984; Wheeler *et al.* 1982).

A physiological study on the effects of succinylcholine chlorides (Scoline) on elephants (Hattingh *et al.* 1984a; 1984b; Hattingh *et al.* 1990a; 1990b) led to the cessation of the use of these compound as a means of culling elephants on humane grounds.

The structure and chemical composition of ivory from KNP has received considerable attention (Prozesky *et al.* 1995; Raubenheimer *et al.* 1989; Raubenheimer *et al.* 1990; Raubenheimer *et al.* 1991; Raubenheimer *et al.* 1995; van Niekerk *et al.* 1988). Whyte & Hall-Martin (In prep.) studied the growth of tusks of KNP elephants.

A scientific bibliography on the National Parks of South Africa was drawn up by Bryden & de Vos (1994).

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CHAPTER 2: THE STUDY AREA

GENERAL

The KNP lies along the eastern borders of the Northern and Mpumalanga provinces (Figure 1) of the Republic of South Africa (RSA). The eastern boundary, which also comprises the international boundary between the RSA and Mozambique, lies along the Lebombo Mountains which are prominent in 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 Luvuvhu and Limpopo rivers for some distance.

Although the KNP had been fenced along its entire periphery by 1978 (see Chapter 4), the fence between KNP and the private reserves on the western boundary between the Sabie and Olifants rivers was removed in 1994 to allow free movement of game. The fence along the Limpopo River has also recently been removed (1999) as it denied animals access to water in the dry season. 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. These fences are discussed in more detail in Chapter 4.

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. In total it covers an area of 18 992 km^2, and lies between the latitudes 22° 20' and 25° 32' south and the longitudes 30° 53' and 32° 02' east. 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.

For administrative purposes the KNP is divided into four regions (see Figure 1). The Far-northern Region lies between the Limpopo and Shingwedzi rivers the Northern Region between the Shingwedzi and the Olifants rivers, the Central Region has as its boundaries the Olifants River in the north and the Sabie River in the south, and the Southern Region which lies between the Sabie and Crocodile rivers.

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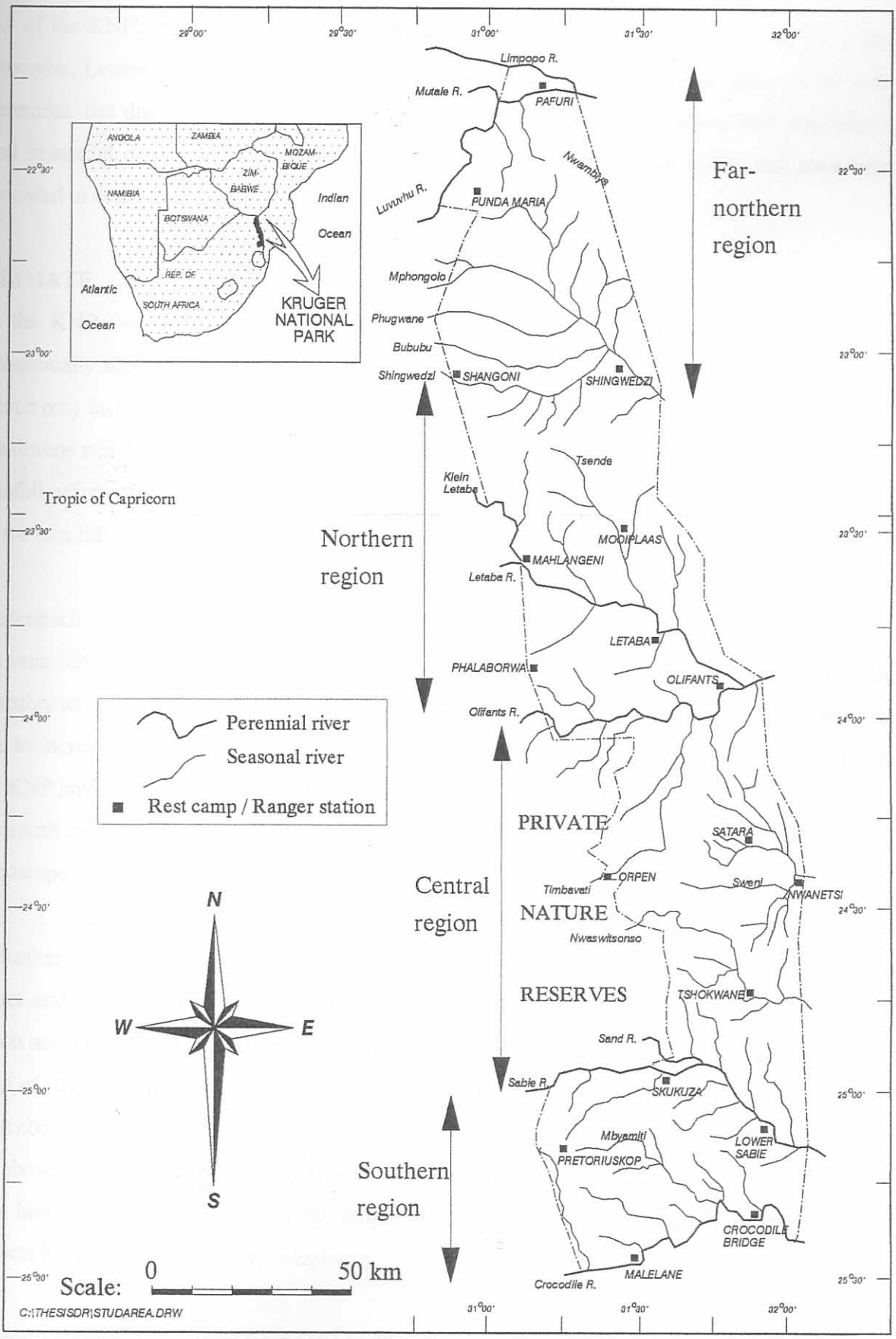


Figure 1: Locality map of the Kruger National Park and the four management regions.

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All of the KNP's major rivers rise in the higher ground to the west. These are the Limpopo, Luvuvhu, Letaba, Olifants, Sabie and Crocodile rivers. In the past, all of these rivers were perennial, but due to the demands of an increasing human population along with agricultural and industrial demands, only the Sabie has remained so. Flows in all of the rest have been recorded to cease and in some, this is now an annual occurrence.

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 Mozambique Channel. Most of this rainfall occurs during the summer months (Figure 2, Table 1) between October and March (84% of the rain falls during these months).

Gertenbach (1980) compiled a rainfall map (Figure 2), showing that rainfall in KNP varies between 450 and 700 mm per annum. 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 (Figure 2). 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. Rainfall figures for individual Landscape types are given below.

Of further interest from the data collated by Gertenbach (1980), 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 (1980) found that the KNP cycle conformed to a large degree to those described by the above authors (Figure 3). The effects of these oscillations on wildebeest populations and their habitat in KNP was shown by Whyte (1985) and Whyte & Joubert (1988), but such impacts have not been shown for elephants.

Generally, temperatures vary from O°C to 40°C though occasionally temperatures beyond these extremes have been recorded. Temperature data from Skukuza and Satara are given in Table 2.

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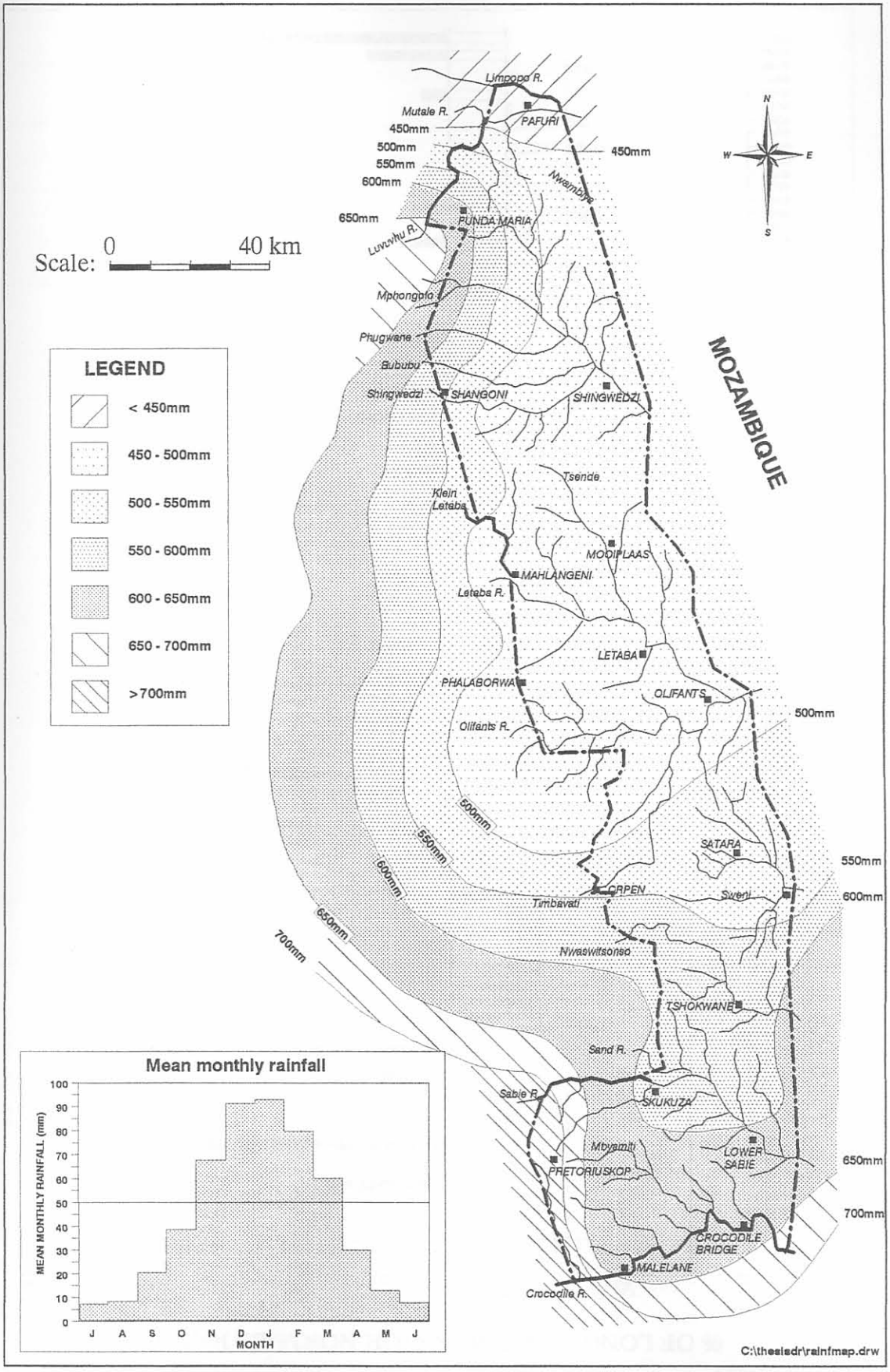


Figure 2: Rainfall map (after Gertenbach 1980) and mean monthly rainfall for all stations in the Kruger National Park.

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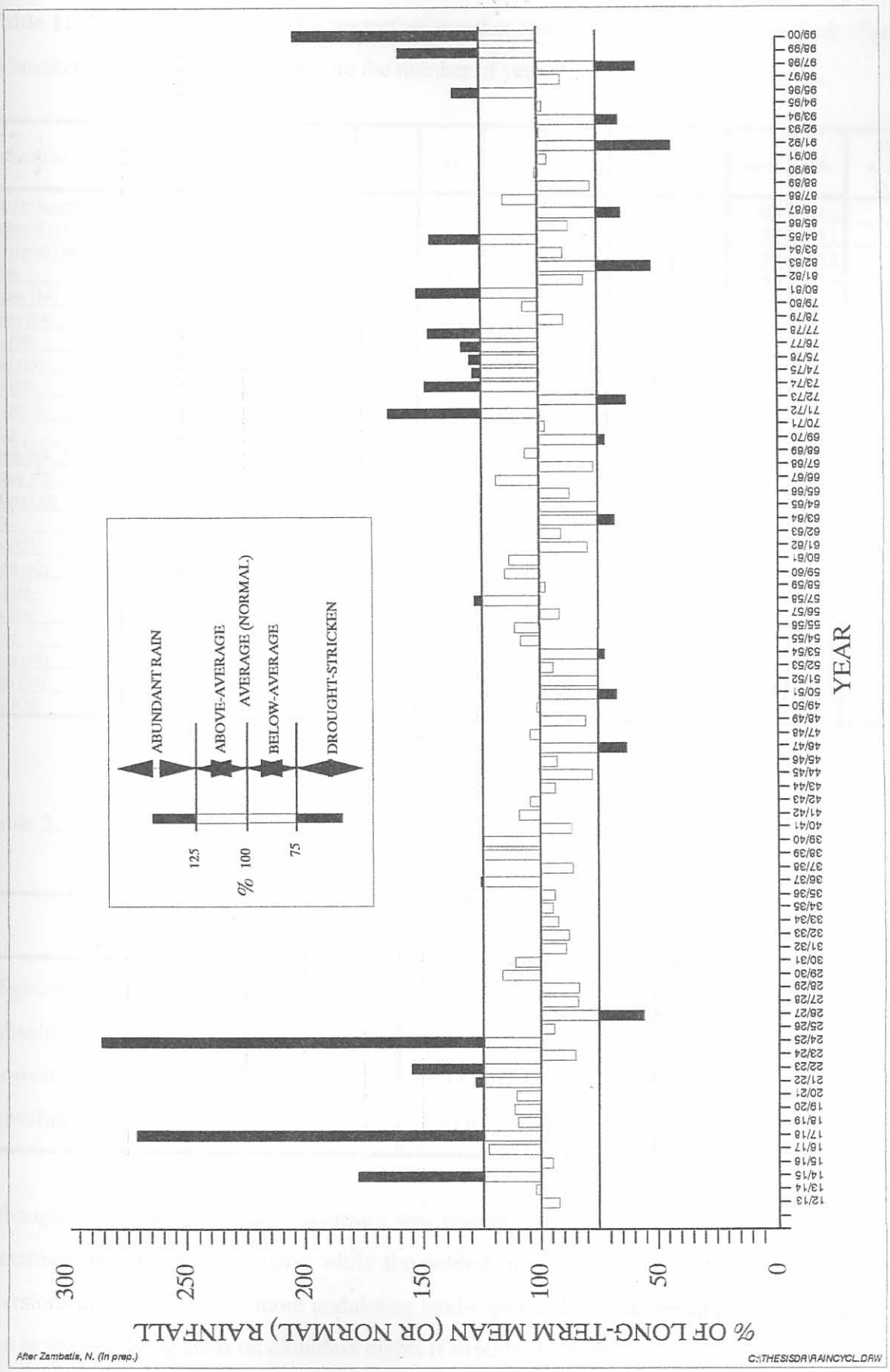


Figure 3: Long-term mean annual rainfall trends in the Kruger National Park between 1913 and 1997.

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Table 1: Rainfall (mm) from the respective weather stations in Kruger National Park (figures in brackets after the station's name are the number of years for which their are records).

STATION	JUL	AUG	SEP	OCT	NOV	DEC	JAN	FEB	MAR	APR	MAY	JUN	MEAN ANNUAL TOTAL
Crocodile Bridge (54)	9.6	7.8	24.3	44.1	80.2	87.7	107.6	100.0	65.2	43.2	18.2	11.2	599.1
Houtboschrand (11)	9.7	10.6	8.8	33.4	66.2	83.0	59.7	48.4	55.7	12.9	8.7	5.1	402.2
Kingfisherspruit (36)	8.3	7.8	20.6	40.4	74.3	93.6	83.8	101.3	62.5	33.8	9.4	8.0	543.8
Letaba (49)	7.6	5.0	18.2	31.9	55.3	91.9	81.0	81.6	38.6	30.3	9.4	3.9	454.7
Lower Sabie (24)	8.7	7.9	24.7	44.3	56.4	86.8	119.8	107.6	62.8	34.2	17.2	11.2	581.6
Mahlangeni (34)	5.8	6.7	4.8	35.8	53.0	90.3	74.7	84.0	46.7	20.2	13.0	4.2	449.2
Malelane (78)	7.6	8.3	21.8	49.6	90.7	93.4	112.1	102.5	89.0	39.3	16.7	7.6	638.6
Mooiplaas (19)	5.7	6.2	15.3	31.1	56.1	77.5	86.9	97.2	45.1	22.2	12.9	2.5	458.7
Nwanetsi (27)	7.4	9.6	22.5	37.0	54.9	90.5	94.6	93.6	63.3	27.0	13.0	7.6	521.0
Olifants (19)	8.6	8.8	16.9	38.3	75.6	75.4	88.5	85.5	47.7	22.4	14.2	3.1	485.0
Pafuri (62)	1.6	4.3	12.3	21.7	52.9	81.3	84.1	83.1	44.7	21.7	8.5	4.7	420.9
Phalaborwa (66)	8.8	5.0	13.5	30.1	63.6	87.6	87.3	79.2	60.7	28.6	8.9	6.8	480.1
Pretoriuskop (52)	9.9	13.3	29.4	53.8	97.8	119.1	125.9	101.0	90.9	51.3	19.0	11.0	722.4
Punda Maria (52)	3.9	4.6	17.1	26.2	70.9	92.3	113.3	104.5	69.7	28.6	12.9	4.6	548.6
Satara (6)	8.6	8.1	21.3	33.9	71.4	89.5	92.6	95.5	66.7	28.2	12.4	9.6	537.8
Shangoni (43)	4.5	3.7	15.0	34.6	63.5	94.0	101.7	98.5	64.6	27.0	12.3	5.4	524.8
Shingwedzi (42)	3.9	4.9	22.6	30.2	54.1	90.6	76.2	91.1	42.8	27.4	11.4	6.3	461.4
Skukuza (74)	10.4	6.2	25.7	34.9	75.9	84.3	92.9	87.4	73.2	33.2	13.5	9.5	547.1
Stols Nek (16)	8.6	11.1	21.2	50.3	85.3	112.4	97.3	96.3	88.3	41.4	8.3	5.7	626.2
Tshokwane	8.0	7.4	21.6	37.9	69.2	103.8	88.8	94.6	68.9	34.6	11.0	9.8	555.6
Vlakteplaas (10)	4.5	8.4	27.1	48.4	64.4	80.3	81.2	71.4	36.7	19.1	6.5	7.1	455.1
Woodlands (10)	3.6	8.8	14.3	39.4	49.8	82.9	74.5	61.9	22.4	19.4	10.4	12.5	399.9
Means for KNP	7.1	7.5	19.5	37.6	67.3	90.4	92.0	89.4	59.4	29.4	12.2	7.2	519.0

Table 2: Temperature (^{O}C) parameters from Skukuza and Satara in Kruger National Park.

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 and this can result in the occurrence of frost in the low-lying areas on cloudless nights (Gertenbach 1983).

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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.

GEOLOGY AND SOILS

The geology and soils have been well studied (see Bristow *et al.*1986; Bristow & Venter1986; Venter 1986; Venter 1990 and references therein).

Broadly speaking, the underlying geology of the KNP, consists of granitic soils in the western half of the Park and basaltic soils in the east, separated in the middle by a narrow belt of sandy Karoo sediments. To the east of the basalts lie the Lebombo Mountains.

DRAINAGE AND WATER

A detailed account of the geomorphology and drainage in the KNP was given by Venter & Bristow (1986).

VEGETATION

Generally speaking, all of the soils in the KNP give rise mainly to deciduous woodlands or savannas. On the granites in the west, broadleaved woodlands occur on the crests of the hills and thornveld in the valleys, while the basalts in the east are much flatter, giving rise to grassy savanna plains with a greater or lesser extent of tree cover - from open grassland to well-wooded savannas. A total of 1982 vascular plants have been collected and identified in the KNP (van Wyk 1984; Zambatis 1997e).

THE LANDSCAPE TYPES AND INCORPORATED ZONATION OF THE KNP

The various landscapes of the KNP have been accepted as the most appropriate ecological units for the consideration and determination of management strategies for the KNP. From this point of view the composition, natural attributes and qualities of the various landscapes, and their perpetuation, are of primary concern in the management of the KNP (Joubert 1986). Detailed descriptions of all the landscapes, including their biotic and abiotic components, boundaries, management priorities and state of development, are therefore considered an essential component of the Masterplan for the Management of the KNP. The Landscapes of the KNP

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were described by Gertenbach 1983.

THE LANDSCAPE TYPES OF THE KNP

This description of the 35 landscapes of the KNP has been summarised from more detailed earlier studies (Coetzee 1983; Gertenbach 1983; Joubert 1986). A brief description of the major ecological features and the zonation of the various landscapes is given to provide a perspective of the ecological diversity of the KNP (see Figure 4).

Landscape 1: Lowveld Sour Bushveld: 336 km^2 (1.8%)

Moderately undulating granitoid plains with *Terminalia sericea* tree savanna.

The annual rainfall for Pretoriuskop is 743.6mm (n = 40 years) range between 600 - 1 000 mm. The vegetation is predominantly large-leafed deciduous woodland and tall (± 1.5m) field layer. In spite of a large variety of species in all the strata the dominants of the various strata include: upper woody strata -*Sclerocarya birrea, Terminalia sericea, Lannea discolor, Piliostigma thonningii*; intermediate strata - *Dichrostachys cinerea* subsp. *nyassana, Strychnos madagascariensis, Ehretia amoena, Peltophorum africanum*; field layer - *Hyperthelia dissoluta, Hyparrhenia* spp., *Diheteropogon amplectens, Loudetia simplex.* Physiognomically the vegetation changed from open savanna to a relatively densely wooded savanna between circa 1935 to 1950.

Landscape 2: Malelane Mountain Bushveld: 452 km^2 (2.4%)

Low granitoid mountains with *Combretum apiculatum* bushveld.

Rainfall varies between 600 - 700 mm per annum, but will probably be as high as 1 000 mm in the higher altitude regions of the mountains. The most common and widely distributed woody plants include *Combretum apiculatum, Acacia nigrescens, Terminalia prunioides* and *T. sericea.* A wide variety of woody plants are present in the landscape, many of which are largely or entirely restricted to the area, e.g. *Kirkia wilmsii, Celtis africana, Aloe bainesii, Tarchonanthus camphorates, Faurea speciosa, Acacia davyii, Calodendrum capense, Strychnos henningsii, Apodytes dimidiata, Homalium dentatum* and several more. A variety of shrubs are common, the most widespread being *Dichrostachys cinerea* subsp. *africana.*

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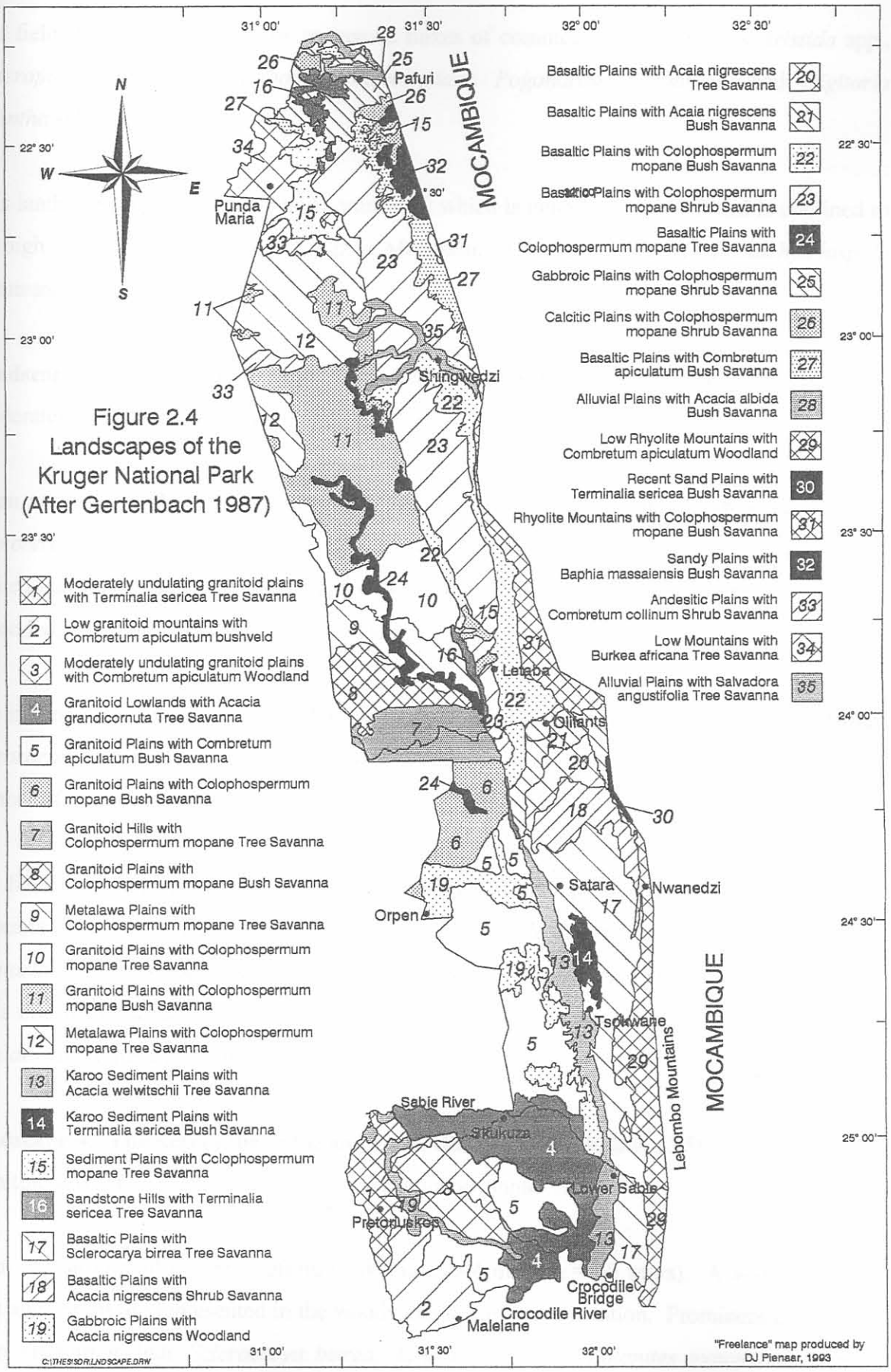


Figure 4: Landscapes of the Kruger National Park (after Gertenbach 1983)

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The field layer is represented by numerous mixes of common grasses, such as *Aristida* spp., *Heteropogon contortus, Cymbopogon plurinoides, Pogonarthria squarrosa* and *Digitaria eriantha* subsp. *pentzi*.

This landscape also includes a plant community which is unique to the KNP and is confined to the high-altitude plateau of the Khandizwe Mountain, i.e. the *Acacia davyii - Tristachya hispida* community

Landscape 3: *Combretum collinum/C. zeyheri* woodland: 537 km^2 (2.8%)

Moderately undulating granitoid plains with *Combretum apiculatum* woodland.

Mean annual rainfall is 600 - 700 mm. The major dominants of the woody vegetation are *Combretum collinum* subsp. *suluense* and *C. zeyheri*. These species, together with a relatively limited number of associated species give the vegetation the general physiognomic character of a wooded, short tree (± 5 m) savanna character.

The intermediate shrub stratum is dominated by species such as *Strychnos madagascariensis, Pterocarpus rotundifolius* and *Dichrostachys cinerea* subsp. *nyassana* in association with a number of other species.

The field layer is generally relatively short (± 1.0m) and is represented by species commonly associated with sandy soils, e.g. *Pogonarthria squarrosa, Perotis patens, Hyperthelia dissoluta, Digitaria eriantha* subsp. *pentzi, Tricholaena monachne,* and others. On the clayey lower-lying areas *Themeda triandra, Heteropogon contortus, Urochloa mosambicensis, Enneapogon cenchroides,* and others, are common.

Landscape 4: Thickets of the Sabie and Crocodile rivers: 1 236 km^2 (6.5%)

Granitoid lowlands with *Acacia grandicornuta* tree savanna.

Mean annual rainfall is 500 - 550 mm (Skukuza: 546 mm; n = 60 years). A wide variety of trees and shrubs are represented in the woody element of the vegetation. Prominent trees in the upper stratum include *Sclerocarya birrea, Acacia nigrescens, Balanites maughami, Lannea stuhlmanni, Combretum apiculatum, Spirostachys africana* and *Ziziphus mucronata.* On the

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brackish, clayey soils *Acacia grandicornuta* and *Terminalia prunioides* are common, while *Acacia nigrescens* is the dominant tree on the soils of the dolerite intrusions.

The dense thorn thickets formed by the shrub layer over large areas is a distinguishing feature of the landscape. Common species include *Dichrostachys cinerea* subsp. *africana, Acacia tortilis, Grewia* spp. and shrub forms of most of the tree species referred to above.

The field layer is well developed on the deeper sandy soils of the watershed areas, but is generally short and relatively sparse in the lower-lying depressions. Common grasses include *Panicum maximum, Pogonarthria squarrosa, Schmidtia pappophoroides* and *Digitaria eriantha* subsp. *pentzii* on the deeper soils and *Urochloa mosambicensis, Chloris virgata* and *Sporobolus nitens* in the depressions. On the dolerite soils rank stands of *Themeda triandra* are common.

Landscape 5: Mixed *Combretum* spp/*Terminalia sericea* Woodland: 1 570 km^2 (8.3%)

Granitoid plains with *Combretum apiculatum* bush savanna.

The mean annual rainfall is 550 - 600 mm. The vegetation generally consists of predominantly low (± 5 m) trees, of which the most common are *Combretum apiculatum, C. zeyheri* and *Terminalia sericea.* Other common trees in the same size group are *Lannea stuhlmanni, Peltophorum africanum* and *Ziziphus mucronata.* The most conspicuous large trees are *Sclerocarya birrea* and *Acacia nigrescens.* Common shrubs in the intermediate stratum include *Strychnos madagascariensis, Dichrostachys cinerea* subsp. *africana, Pterocarpus rotundifolius, Dalbergia melanoxylon* and *Ormocarpum trichocarpum.*

On the watersheds the relatively sparse field layer (± 1.0 m tall) is comprised of grasses common to sandy soils, e.g. *Pogonarthria squarrosa, Digitaria eriantha* subsp. *pentzii, Panicum maximum, Perotis patens, Tricholaena monachne* and *Brachiaria* spp. In the lower-lying depressions grass species such as *Urochloa mosambicensis, Schmidtia pappophoroides, Heteropogon contortus* and *Enneapogon cenchroides* are common.

Over extensive areas of this landscape a characteristic feature is a clearly defined corollary of *Terminalia sericea* trees along the seepline on the lower slopes, presenting a clear divide be-

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tween the watershed plant communities and those of drainage valleys.

Landscape 6: *Combretum* spp./*Colophospermum mopane* Woodland of the Timbavati area: 467 km^2 (2.5%)

Granitoid plains with *Colophospermum mopane* bush savanna.

Mean annual precipitation is between 450 and 550 mm. The vegetation on the higher-lying areas of the watersheds is dominated by *Combretum apiculatum,* while associated species include *Terminalia sericea, Sclerocarya birrea, Albizia harveyi, Acacia exuvialis, Dalbergia melanoxylon* and *Dichrostachys cinerea* subsp. *africana.* On the lower slopes, and in association with the higher clay content of the soils, *Colophospermum mopane* becomes more dominant. Other associated trees and shrubs include *Combretum* apicu*latum, C. hereroense, Acacia nigrescens, A. gerrardi, Euclea divinorum, Bolusanthus speciosus* and *Terminalia prunioides.*

In the higher-lying areas grasses typical of more sandy soils are common, including *Pogonarthria squarrosa, Digitaria eriantha* var. *pentzii, Brachiaria serrata, Rhynchelytrum repens* and *Tricholaena monachne.* Other common grasses are *Heteropogon contortus, Enneapogon cenchroides, Schmidtia pappophoroides* and *Panicum maximum.* In the more clayey areas *Themeda triandra, Urochloa mosambicensis, Cymbopogon plurinodis, Panicum coloratum* and *Bothriochloa radicans* are common.

Landscape 7: Olifants River Rugged Veld: 358 km^2 (1.9%)

Granitoid hills with *Colophospermum mopane* tree savanna.

Mean annual rainfall is approximately 450 - 500 mm. Composition - The woody vegetation is dominated by *Colophospermum mopane* and *Combretum apiculatum.* Common associated species include *Terminalia prunioides, Boscia albitrunca, Acacia nigrescens, Sclerocarya birrea, Commiphora mollis, C. africana* and *Dalbergia melanoxylon.*

Common grasses include *Rhynchelytrum repens, Sporobolus panicoides, Enneapogon cenchroides, Bothriochloa radicans, Digitaria eriantha* var. *pentzii, Aristida* spp., *Cymbopogon plurinodis* and *Panicum maximum.*

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Physiognomy - The woody vegetation generally attains a height of approximately 5.0m, with a sparse distribution of tall prominent trees. The density of trees is relatively high, resulting in a relatively densely wooded savanna. The field layer is generally sparse with a relatively low ground cover (50 - 70%) and approximately 0.5 to 1.0 m tall.

Landscape 8: Phalaborwa Sandveld: 394 km^2 (2.1%)

Granitoid plains with *Terminalia sericea/Colophospermum mopane* bush savanna.

Mean annual rainfall is approximately 450 - 500 mm. The long term mean for Phalaborwa is 481 mm (n = 54 years). Due to the deep sandy nature of the soils the distinctive woody plant of the landscape is *Terminalia sericea.* Other common woody plants include *Colophospermum mopane, Combretum apiculatum, C. zeyheri, C. imberbe, Sclerocarya birrea, Acacia nigrescens Peltophorum africanum, Pseudolachnostylis maprouneifolia* and *Bolusanthus speciosus.*

Common grasses include *Andropogon gayanus, Digitaria eriantha* var. *pentzii, Pogonarthria squarrosa, Brachiaria nigropedata, Heteropogon contortus, Aristida* spp., *Panicum maximum, Rhynchelytrum repens, Urochloa mosambicensis, Cymbopogon plurinodis, Themeda triandra, Enneapogon cenchroides* and *Bothriochloa radicans.*

Landscape 9: *Colophospermum mopane* Savanna on Basic Soils: 543 km^2 (2.9%)

Metalava plains with *Colophospermum mopane* tree savanna.

Mean annual rainfall is approximately 450 - 500 mm. The dominant woody plant is *Colophospermum mopane,* which occurs in almost homogeneous stands over large areas. Other associated trees and shrubs include *Combretum apiculatum, Acacia nigrescens, Albizia harveyi, Combretum imberbe, Lannea stuhlmanni, Ozoroa engleri* and *Mundulea sericea.*

Common grasses in the field layer are *Themeda triandra, Digitaria eriantha* var. *pentzii, Schmidtia pappaphoroides, Bothriochloa radicans, Panicum coloratum, P. maximum* and *Urochloa mosambicensis.*

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Landscape 10: Letaba River Rugged Veld: 697 km^2 (3.7%.)

Granitoid plains with *Colophospermum mopane* bush savanna.

The mean annual rainfall is approximately 450 - 500 mm with the long term mean for Mahlangeni 490 mm (n = 20 years). Composition - The vegetation largely resembles that of the Olifants River Rugged Veld (Landscape 7). Predominant trees and shrubs include *Colophospermum mopane, Combretum apiculatum, Terminalia prunioides, Acacia nigrescens, Combretum imberbe, Dichrostachys cinerea* subsp. *africana, Grewia* spp. and *Mundulea sericea.*

Common grasses in the field layer include *Bothriochloa radicans, Aristida* spp., *Enneapogon cenchroides* and *Urochloa mosambicensis.* The forb, *Hemizygia elliotii,* is a prominent feature in the field layer of this landscape.

Landscape 11: Tsende Sandveld: 1 150 km^2 (5.5%.)

Granitoid plains with *Colophospermum mopane* bush savanna.

The mean annual precipitation is approximately 450 - 500 mm, with the long term mean for Shangoni 572 mm (n = 37 years). The dominant woody plants are *Colophospermum mopane* and *Combretum apiculatum,* the former being most dominant on the watersheds. Due to deep sandy soils *Terminalia sericea* is also locally conspicuous. Other common associated trees and shrubs include *Acacia nigrescens, Sclerocarya birrea, Combretum hereroense, Peltophorum africanum, Dichrostachys cinerea* subsp. *africana, Albizia harveyi, Strychnos madagascariensis* and *Dalbergia melanoxylon.*

Common grasses in the field layer include: *Cymbopogon plurinodis, Digitaria eriantha* var. *pentzii, Panicum maximum, Heteropogon contortus, Bothriochloa radicans, Urochloa mosambicensis, Eragrostis superba, Brachiaria nigropedata* and *Andropogon gayanus.*

Landscape 12: *Colophospermum mopane/Acacia nigrescens* Savanna: 1 037 km^2 (5.5%)

Metalava plains with *Colophospermum mopane* tree savanna.

The mean annual rainfall is approximately 500 - 600 mm. Common trees and shrubs include

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Colophospermum mopane, Combretum apiculatum, Acacia nigrescens A. gerrardii, Euclea divinorum, Combretum hereroense, C. collinum subsp. *suluense* and *Maytenus heterophylla.* In Landscape 33 *Pterocarpus rotundifolius* is dominant, with other distinctive species including *Combretum collinum* subsp. *suluense, C. molle, C. apiculatum, Lannea discolor, Dombeya rotundifolia, Lonchocarpus capassa* and *Ozoroa engleri.*

Common grasses in the field layer include: *Themeda triandra, Bothriochloa radicans, Digitaria eriantha* var. *pentzii, Panicum maximum, Setaria holstii, Urochloa mosambicensis, Brachiaria nigropedata, Eragrostis rigidior, Panicum coloratum* and *Heteropogon contortus.*

Landscape 13: *Acacia welwitschii* Thickets on Karoo Sediments: 517 km^2 (2.7%)

Karoo sediment plains with *Acacia welwitschii tree savanna*

There is no measuring station in this Landscape but the mean is expected to be approximately 500 - 600 mm. The major woody plant species include *Acacia welwitschii* subsp. *delagoensis, Albizia petersiana* subsp. *evansii, Euclea divinorum, Boscia mossambicensis, Dichrostachys cinerea* subsp. *africana, Grewia bicolor, Capparis tomentosa* and *Spirostachys africana.* In the more sandy areas *Terminalia sericea, Albizia forbesii, A. harveyi, Peltophorum africanum, Lannea stuhlmanni* and *Schotia brachypetala* are conspicuous. Common grasses of the field layer include: *Urochloa mosambicensis, Enteropogon macrostachyus, Sporobolus nitens, S. smutsii, Bothriochloa radicans, Tragus berteronianus, Chloris virgata, Dactyloctenium aegypteum, Digitaria eriantha* var. *pentzii, Pogonarthria squarrosa, Eragrostis rigidior* and *Schmidtia pappaphoroides.*

Landscape 14: Kumana Sandveld: 193 km^2 (1.0%)

Karoo sediment plains with *Terminalia sericea* bush savanna.

There is no measuring station in this Landscape but the mean is expected to be approximately 500 - 600 mm. The major woody plant species include *Acacia welwitschii* subsp. *delagoensis, Albizia petersiana* subsp. *evansii, Euclea divinorum, Boscia mossambicensis, Dichrostachys cinerea* subsp. *africana, Grewia bicolor, Capparis tomentosa* and *Spirostachys africana.* In the more sandy areas *Terminalia sericea, Albizia forbesii, A. harveyi, Peltophorum africanum, Lannea stuhlmanni* and *Schotia brachypetala* are conspicuous. Common grasses of the field

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layer include: *Urochloa mosambicensis, Enteropogon macrostachyus, Sporobolus nitens, S. smutsii, Bothriochloa radicans, Tragus berteronianus, Chloris virgata, Dactyloctenium aegypteum, Digitaria eriantha* var. *pentzii, Pogonarthria squarrosa, Eragrostis rigidior* and *Schmidtia pappaphoroides.*

Landscape 15: *Colophospermum mopane* Forest: 267 km^2 (1.4%)

Sedimentary plains with *Colophospermum mopane* tree savanna.

There is no measuring station in this Landscape but the mean is expected to be approximately 500 - 550mm. The major trees and shrubs include *Colophospermum mopane, Spirostachys africana, Acacia nigrescens, Euclea divinorum, Tilachium africanum, Acacia tortilis, Combretum imberbe* and *C. hereroense.*

Common grasses in the field layer include: *Enteropogon macrostachyus, Enneapogon cenchroides, Panicum maximum, Urochloa mosambicensis*, *Digitaria eriantha* var. *pentzii* and *Schmidtia pappophoroides.*

Landscape 16: Punda Maria Sandveld on cave Sandstone: 116 km^2 (0.6%)

There is no measuring station in this Landscape but the mean is expected to be approximately 450 - 550 mm.

Distinctive trees and shrubs of this landscape include: *Adansonia digitata, Colophospermum mopane, Combretum apiculatum, Boscia albitrunca, B. angustifolia, Terminalia sericea, Acacia nigrescens,* in addition to species characteristic of kopjies and rocky ridges, e.g. *Steganotaenia araliacea, Kirkia acuminata, Ficus soldanella, Maerua angolensis, Sterculea rogersii, Entandrophragma caudatum, Acokanthera schimperi* var. *rotundata, Boscia foetida* subsp. *rehmanniana, Androstachys johnsonii, Markhamia acuminata* and *Gyrocarpus americanus.* In terms of the relative species composition of the various landscapes of the KNP, Landscape 16 is particularly rich in species diversity. The variety of *Commiphora* spp. is a distinctive feature. *C. merkeri, C. tenuipetiolata* and *C. marlothii* are distinctive.

A particularly prominent feature of this landscape is the numerous conspicuous, almost homogeneous stands of *Androstachys johnsonii.*

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Common grasses of the field layer include: *Digitaria eriantha* var. *pentzii, Brachiaria serrata, Pogonarthria squarrosa, Perotis patens, Schmidtia pappaphoroides, Aristida* spp., *Bothriochloa radicans, Enneapogon cenchroides, Heteropogon contortus* and *Fingerhutia africana.*

Landscape 17: *Sclerocarya birrea/Acacia nigrescens* Savanna: 1 404 km^2 (7.4%)

The mean annual rainfall diminishes from south to north and is generally approximately 500 - 600 mm. Recorded mean annual rainfall for stations within this landscape is: Crocodile Bridge 599 mm (n = 40 years), Tshokwane 561 mm (n = 43 years) and Satara 548 mm (n = 46 years). Trees and shrubs characteristic of this landscape include *Sclerocarya birrea, Acacia nigrescens, A. gerrardi, Lonchocarpus capassa, Dichrostachys cinerea* subsp. *africana, Lannea stuhlmanni, Maytenus heterophylla* and *Pterocarpus rotundifolius.*

Common grasses in the field layer include: *Themeda triandra, Bothriochloa radicans, Panicum coloratum, P. maximum, Digitaria eriantha* var. *pentzii, Heteropogon contortus* and *Urochloa mosambicensis.*

Landscape 18: Dwarf *Acacia nigrescens* Savanna: 354 km^2 (1.9%)

The mean annual rainfall is approximately 500 - 550 mm. Composition - The dominant woody plant species is *Acacia nigrescens,* in association with, amongst others, *Cordia sinensis, Ehretia rigida, Dichrostachys cinerea* subsp. *africana* and *Securinega virosa.* Common grasses in the field layer include: *Themeda triandra, Ischaemum brachyatherum, Setaria woodii, Panicum coloratum, P. maximum, Sorghum versicolor, Digitaria eriantha* var. *pentzii* and *Urochloa mosambicensis.* The landscape is also noted for a number of dense shrub stands, consisting primarily of *Acacia borleae.*

Landscape 19: Thornveld on Gabbro: 682 km^2 (3.6%)

The mean annual rainfall in the area to the south of the Olifants River is approximately 500 - 600 mm (with the rainfall diminishing from south to north) and north of the Olifants River it is 450 - 500 mm.

Composition - In the area to the south of Red Gorten the woody vegetation is comprised predominantly of *Acacia nigrescens,* while other important trees and shrubs include *Sclerocarya*

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birrea, Ziziphus mucronata, Bolusanthus speciosus, Securinega virosa, Ormocarpum trichocarpum, Dalbergia melanoxylon and *Acacia tortilis.* In the northern areas the dominant woody species is *Colophospermum mopane* in association with most of the species mentioned above.

Common grasses in the field layer include: *Themeda triandra, Cenchrus ciliaris, Bothriochloa radicans, Digitaria eriantha* var. *pentzii, Enneapogon cenchroides, Chloris virgata, Heteropogon contortus, Cymbopogon plurinodis, Schmidtia pappophoroides, Panicum coloratum* and *Eragrostis superba.*

Landscape 20: Bangu Rugged Veld: 203 km^2 (1.1%)

Basaltic plains with *Acacia nigrescens* tree savanna.

The mean annual rainfall is believed to be slightly higher in Landscape 20, i.e. 500 - 550 mm, than in Landscape 21, i.e. 450 - 500 mm. Composition - common trees and shrubs for these landscapes include *Acacia nigrescens, Acacia senegal* var. *leiorhachis Grewia bicolor, Combretum apiculatum, Terminalia prunioides, Acacia exuviales, A. tortilis, Dichrostachys cinerea* subsp. *africana, Combretum mossambicense, Sterculea rogersii, Manilkara mochisia, Kirkia acuminata, Boscia albitrunca, Commiphora africana* and *C. glandulosa.*

Common grasses of the field layer include: *Panicum coloratum, Enneapogon cenchroides, Bothriochloa radicans, Schmidtia papophoroides, Heteropogon contortus, Sporobolus nitens* and *Aristida* spp.

Landscape 21: *Combretum* spp./*Acacia* spp. Rugged Veld: 269 km^2 (1.4%)

Basaltic plains with *Acacia nigrescens* bush savanna.

The mean annual rainfall is believed to be slightly higher in Landscape 20, i.e. 500 - 550 mm, than in Landscape 21, i.e. 450 - 500 mm. Composition - common trees and shrubs for these landscapes include *Acacia nigrescens, Acacia senegal* var. *leiorhachis Grewia bicolor, Combretum apiculatum, Terminalia prunioides, Acacia exuviales, A. tortilis, Dichrostachys cinerea* subsp. *africana, Combretum mossambicense, Sterculea rogersii, Manilkara mochisia, Kirkia acuminata, Boscia albitrunca, Commiphora africana* and *C. glandulosa.*

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Common grasses of the field layer include: *Panicum coloratum, Enneapogon cenchroides, Bothriochloa radicans, Schmidtia papophoroides, Heteropogon contortus, Sporobolus nitens* and *Aristida* spp.

Landscape 22: *Combretum* spp./*Colophospermum mopane* Rugged Veld: 890 km^2 (4.7%.)

Basaltic plains with *Colophospermum mopane* bush savanna.

The mean annual rainfall is approximately 450 - 500 mm. The long term means for two recording stations within the landscape are: Letaba - 462 mm (n = 51 years) and Shingwedzi - 472 mm (n = 37 years). The major trees and shrubs include *Colophospermum mopane, Combretum apiculatum, C. imberbe, C. mossambicense, Terminalia prunioides, Acacia nigrescens, Albizia harveyi, Sterculea rogersii, Sclerocarya birrea, Securinega virosa* and *Hymenodictyon parvifolium.*

Common grasses of the field layer include: *Enneapogon cenchroides, Bothriochloa radicans, Aristida* spp., *Urochloa mosambicensis, Schmidtia pappophoroides, Digitaria eriantha* var. *pentzii, Heteropogon contortus* and *Cenchrus ciliaris.*

Landscape 23: *Colophospermum mopane* Shrubveld on Basalt: 1 983 km^2 (10.4%)

Basaltic plains with *Colophospermum mopane* shrub savanna.

There is no measuring station in this Landscape but the mean is expected to be approximately 450 - 500 mm. The woody vegetation is dominated by *Colophospermum mopane,* in association with *Combretum imberbe, Acacia nigrescens, Dichrostachys cinerea* subsp. *africana, Securinega virosa, Commiphora glandulosa, Sclerocarya birrea, Lonchocarpus capassa, Dalbergia melanoxylon* and *Gossypium herbacaum.*

Common grasses in the field layer include: *Themeda triandra, Panicum coloratum, Cenchrus ciliaris, Eragrostis superba, Bothriochloa radicans, Setaria woodii, Schmidtia pappophoroides* and *Heteropogon contortus.*

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Landscape 24: *Colophospermum mopane* Shrubveld on Gabbro: 283 km^2 (1.5%)

The mean annual rainfall in the area to the south of the Olifants River is approximately 500 - 600 mm (with the rainfall diminishing from south to north) and north of the Olifants River it is 450 - 500 mm. In the area to the south of Red Gorten the woody vegetation is comprised predominantly of *Acacia nigrescens,* while other important trees and shrubs include *Sclerocarya birrea, Ziziphus mucronata, Bolusanthus speciosus, Securinega virosa, Ormocarpum trichocarpum, Dalbergia melanoxylon* and *Acacia tortilis.* In the northern areas the dominant woody species is *Colophospermum mopane* in association with the species mentioned above.

Common grasses in the field layer include: *Themeda triandra, Cenchrus ciliaris, Bothriochloa radicans, Digitaria eriantha* var. *pentzii, Enneapogon cenchroides, Chloris virgata, Heteropogon contortus, Cymbopogon plurinodis, Schmidtia pappophoroides, Panicum coloratum* and *Eragrostis superba.*

Landscape 25: *Adansonia digitata/Colophospermum mopane* Rugged veld: 323 km^2 (1.7%)

Gabbroic plains with *Colophospermum mopane* shrub savanna.

There is no measuring station in this Landscape but the mean is expected to be approximately 450 - 550 mm. Distinctive trees and shrubs in this landscape include: *Adansonia digitata, Colophospermum mopane, Combretum apiculatum, Boscia albitrunca, B. angustifolia, Terminalia sericea, Acacia nigrescens,* in addition to species characteristic of kopjes and rocky ridges, e.g. *Steganotaenia araliacea, Kirkia acuminata, Ficus soldanella, Maerua angolensis, Sterculea rogersii, Entandrophragma caudatum, Acokanthera schimperi* var. *rotundata, Boscia foetida* subsp. *rehmanniana, Androstachys johnsonii, Markhamia acuminata* and *Gyrocarpus americanus.*

A prominent feature of this landscape is the numerous conspicuous, almost homogeneous stands of *Androstachys johnsonii.*

Common grasses of the field layer include: *Digitaria eriantha* var. *pentzii, Brachiaria serrata, Pogonarthria squarrosa, Perotis patens, Schmidtia pappaphoroides, Aristida* spp., *Bothriochloa radicans, Enneapogon cenchroides, Heteropogon contortus* and *Fingerhutia africana.*

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Landscape 26: *Colophospermum mopane* Shrubveld on Calcrete: 116 km^2 (0.6%)

Calcitic plains with *Colophospermum mopane* shrub savanna.

There is no measuring station in this Landscape but the mean is expected to be approximately 450 - 550 mm. Distinctive trees and shrubs in this landscape include: *Adansonia digitata, Colophospermum mopane, Combretum apiculatum, Boscia albitrunca, B. angustifolia, Terminalia sericea, Acacia nigrescens,* in addition to species characteristic of kopjes and rocky ridges, e.g. *Steganotaenia araliacea, Kirkia acuminata, Ficus soldanella, Maerua angolensis, Sterculea rogersii, Entandrophragma caudatum, Acokanthera schimperi* var. *rotundata, Boscia foetida* subsp. *rehmanniana, Androstachys johnsonii, Markhamia acuminata* and *Gyrocarpus americanus.*

A particularly prominent feature of this landscape is the numerous conspicuous, almost homogeneous stands of *Androstachys johnsonii.*

Common grasses of the field layer include: *Digitaria eriantha* var. *pentzii, Brachiaria serrata, Pogonarthria squarrosa, Perotis patens, Schmidtia pappaphoroides, Aristida* spp., *Bothriochloa radicans, Enneapogon cenchroides, Heteropogon contortus* and *Fingerhutia africana.*

Landscape 27: Mixed *Combretum/Colophospermum mopane* Woodland: 327 km^2 (1.7%)

Basaltic plains with *Combretum apiculatum* bush savanna.

The mean annual rainfall is approximately 450 - 500 mm. Dominant trees and shrubs include: *Colophospermum mopane, Sclerocarya birrea, Combretum apiculatum, C. zeyheri, C. mossambicense, Securinega virosa, Dichrostachys cinerea* subsp. *africana, Grewia bicolor, Acacia nigrescens* and *Lonchocarpus capassa.*

Common grasses in the field layer include: *Digitaria eriantha* var. *pentzii, Schmidtia pappophoroides, Aristida* spp., *Urochloa mosambicensis, Panicum maximum* and *Heteropogon contortus.*

Landscape 28: The Luvuvhu - Limpopo Complex: 89 km^2 (0.5%)

Alluvial plains with *Acacia albida* bush savanna.

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This area represents the most arid part of the KNP with a mean annual rainfall at Pafuri of 438 mm (n = 50 years). Other than for the floodplains, the composition and physiognomy of the vegetation is similar to that of landscapes 16, 25 and 27. For the floodplains the vegetation is comprised of the following: Composition - The major trees and shrubs include: *Acacia albida, A. xanthophloea, A. tortilis, Ficus sycomorus, Hyphaene natalensis, Azima tetracantha, Thilachium africanum, Gardenia resiniflua, Garcinia livingstonei, Trichilia emetica, Xanthocercis zambesiaca, Acacia robusta, A. ataxacantha, Kigelia africana, Breonadia microcephala, Tabernaemontana elegans, Ficus capreifolia, Lonchocarpus capassa, Strychnos potatorum, Mimusops zeyheri, Diospyros mespiliformis* and *Boscia albitrunca.*

Common grasses in the field layer include: *Panicum meyerianum, Echinochloa pyramidalis, Chloris gayana, Sporobolus consimilis, Ischaemum afrum, Setaria sphacelata, Dactyloctenium aegypteum, Sporobolus smutsii* and *Enneapogon cenchroides.*

Landscape 29: Lebombo South: 761 km^2 (4.0%)

Low rhyolite mountains with *Combretum apiculatum* woodland.

The mean annual rainfall diminishes from south to north and is approximately 650 - 700 mm in the southern areas and 450 - 550 mm in the north. A number of distinctive plant communities are apparent and on a general basis the following trees and shrubs are common: *Combretum apiculatum, Pterocarpus rotundifolius, Sclerocarya birrea, Acacia nigrescens, Dichrostachys cinerea* subsp. *africana, Albizia harveyi, Securinega virosa, Ozoroa engleri, Acacia exuvialis, Euphorbia confinalis, E. cooperi, Terminalia phanerophlebia, Acacia erubescens, Galpinia transvaalica, Sideroxylon inerme, Ziziphus rivularis* and *Portulacaria afra.*

Common grasses in the field layer include: *Digitaria eriantha* var. *pentzii, Andropogon gayanus, Themeda triandra, Enneapogon cenchroides, Panicum maximum, Schmidtia pappophoroides, Aristida* spp., *Brachiaria xantholeuca, B. nigropedata* and *Bothriochloa radicans.*

Landscape 30: Pumbe Sandveld: 176 km^2 (0.6%)

Recent sand plains with *Terminalia sericea* bush savanna.

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There is no measuring station in this Landscape but the mean is expected to be approximately 450 - 550 mm. The common trees and shrubs include *Combretum zeyheri, C. apiculatum, C. molle, Terminalia sericea, Cassia abbreviata, Lonchocarpus capassa, Lannea stuhlmanni, Diospyros natalensis, Afzelia cuanzensis* and *Pseudolachnostylis maprouneifolia.*

Common grasses in the field layer include: *Digitaria eriantha* var. *pentzii, Andropogon gayanus, Themeda triandra, Enneapogon cenchroides, Panicum maximum, Schmidtia pappophoroides, Aristida* spp., *Brachiaria xantholeuca, B. nigropedata* and *Bothriochloa radicans.*

Landscape 31: Lebombo North: 478 km^2 (2.5%)

Rhyolite mountains with *Colophospermum mopane* bush savanna.

The distinguishing feature between the northern and southern Lebombo landscapes is the lower rainfall in the former. The mean annual rainfall is approximately 450 - 500 mm. In general the composition of the vegetation is similar to that of Landscape 29. Due to the lower rainfall there are, however, more zeric elements. One of the main distinguishing features is the presence of *Colophospermum mopane* and the numerous *Androstachys johnsonii* thickets, especially in the rugged areas to the south and north of the Olifants River. Rare trees and shrubs that occur in the Bangu Gorge area and to the north of the Olifants River include *Newtonia hildebrandtii, Atalaya alata, Stadmannia oppositifolia, Sesamothamnus lugardii* and *Euphorbia grandicornis.*

In the field layer grasses such as *Enneapogon cenchroides, Schmidtia pappophoroides, Digitaria eriantha* var. *pentzii, Andropogon gayanus, Bothriochloa radicans, Aristida* spp. and *Heteropogon contortus* are common.

Landscape 32: Nwambiya Sandveld: 138 km^2 (0.7%)

Sandy plains with *Bafia massaiensis* bush savanna.

Mean annual rainfall is probably approximately 500 mm. The Nwambiya Sandveld is noted for its wide variety of woody plant species, and also for a number of species which show affinities with the more tropical vegetation to the north. Common and important species include: *Baphia*

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massaiensis, Guibourtia conjugata, Xeroderris stuhlmanni, Xylia torreana, Combretum celastroides, Spirostachys africana, Pteleopsis myrtifolia, Strychnos madagascariensis, Afzelia quanzensis, Terminalia sericea, Balanites maughamii and *Sclerocarya birrea.* Some rarer species also include *Wrightia natalensis, Dalbergia nitidula, Pterocarpus lucans* subsp. *antunesii, Cleistanthus schlechteri, Drypetes mossambicensis, Xylotheca kraussiana, Leptactinia benguelensis, Hugonia orientalis* and *Monodora junodii.*

Common grasses in the field layer include *Digitaria eriantha* var. *pentzii, Pogonarthria squarrosa, Panicum maximum, Aristida* spp., *Schmidtia pappophoroides, Tricholaena monachne, Eragrostis pallens* and *Perotis patens.*

Landscape 33: *Pterocarpus rotundifolius/Combretum collinum* Woodland: 279 km^2 (1.5%)

Andesitic plains with *Combretum collinum* shrub savanna, this Landscape is comprised of two discontinuous sections to the north and south of Landscape 12.

The mean annual rainfall is approximately 500 - 600 mm. Common trees and shrubs include *Colophospermum mopane, Combretum apiculatum, Acacia nigrescens A. gerrardii, Euclea divinorum, Combretum hereroense, C. collinum* subsp. *suluense* and *Maytenus heterophylla.* In Landscape 33 *Pterocarpus rotundifolius* is dominant, with other distinctive species including *Combretum collinum* subsp. *suluense, C. molle, C. apiculatum, Lannea discolor, Dombeya rotundifolia, Lonchocarpus capassa* and *Ozoroa engleri.*

Common grasses in the field layer include: *Themeda triandra, Bothriochloa radicans, Digitaria eriantha* var. *pentzii, Panicum maximum, Setaria holstii, Urochloa mosambicensis, Brachiaria nigropedata, Eragrostis rigidior, Panicum coloratum* and *Heteropogon contortus.*

Landscape 34: Punda Maria Sandveld on Waterberg Sandstone: 296 km^2 (1.6%)

Low mountains with *Burkea africana* tree savanna.

There is no measuring station in this Landscape but the mean is expected to be approximately 600 mm. The long term mean for Punda Maria is 587 mm (n = 51 years). Important trees and shrubs include: *Burkea africana, Pseudolachnostylis maprounaeifolia, Pteleopsis myrtifolia, Hymenocardia ulmoides, Holarrhena pubescens, Diplorrhynchus condylocarpon, Peltophorum*

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africanum, Hexalobus monopetalus, Guibourtia conjugata, Combretum collinum, C. zeyheri, C. apiculatum, Afzelia quanzensis, Bridelia mollis, Brachylaena huillensis, Ficus sansibarica, F. capensis, Xylopia odoratissima, Gyrocarpus americanus, Albizia adiantifolia, A. tanganyicensis, Acacia polyacantha subsp. *campylacantha, A. sieberiana* var. *woodii, Piliostigma thonningii, Xanthocercis zambeziaca, Kirkia acuminata, Entandrophragma caudatum, Ekebergia capensis, Trichilia emetica, Drypetes gerrardii, Bridelia micrantha, Warburgia salutaris, Diplorrhynchus condylocarpon, Tabernaemontanum elegans, Rauvolfia caffra, Cordia grandicalyx, Markhamia acuminata, Breonadia microcephala, Kigelia africana* and *Rothmannia fischeri.*

Common grasses of the field layer include: *Andropogon gayanus, Panicum maximum, Digitaria eriantha* var. *pentzii, Pogonarthria squarrosa, Panicum deustum, Cymbopogon excavatus, Setaria sphacelata* and *Themeda triandra.*

Landscape 35: *Salvadora angustifolia* Floodplains: 132 km^2 (0.7%)

Alluvial plains with *Salvadora angustifolia* tree savanna.

This landscape is largely confined to the lower reaches of the Shingwedzi, Bububu, Mphongolo and Phugwane rivers. As it is restricted to the deep alluvial soils it represents relatively narrow strips on the banks of the rivers, and can best be included incorporated with Landscapes 11, 12, 22 and 23. Although not as well developed as in the areas mentioned above, this landscape is also represented along the Madzaringwe River.

The vegetation is characterised by tall *Colophospermum mopane* trees (± 10.0m) and a well-developed shrub stratum with conspicuous species including *Salvadora angustifolia, Capparis tomentosa, Thilachium africanum, Acacia tortilis, Euclea divinorum* and *Hyphaene natalensis.* The field layer is sparse, short and relatively poorly developed.

The landscape represents an important winter refuge for elephants, buffalo and a wide variety of larger mammals attracted to the rivers.

FIRE

Fire management practices have undergone radical changes in the KNP since the arrival of the

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first warden in 1903. This has varied from attempts at total protection from fire to rigid burning frequencies regardless of the condition of the field layer in terms of either species composition or fuel loads (Joubert 1986). The reasons for this are that fire is, and has always been, a contentious issue in conservation as a result of the obvious short-term "damage" they cause and a misunderstanding or ignorance of the longer-term beneficial effects. In many ways this ignorance persists, as little is yet known of the much longer-term potential impacts of fire on biodiversity (Viljoen 1988), or how to best manage fire to maximise biodiversity.

Considerable research has been conducted into the various aspects of fires in KNP in order to address these issues. Earlier research results (Van der Schijff 1958; van Wyk 1971; Trollope 1994) gave rise to more modern thinking and stimulated much additional research effort (Trollope *et al.* 1996; Trollope *et al.* 1998; Trollope *et al.* 1999).

The forty-year era of rotational block burning was replaced by a lightning-driven fire policy in 1992 in which lightning fires were allowed to burn while man made (anthropomorphic) fires were extinguished. The recent revision of the management plan (Braack, van Wilgen, Biggs & Potgieter 1997) condoned the lightning based approach, but stressed the necessity of maximising research to allow for other approaches in future changes to the fire policy. A major landscape-scale fire management trial was thus implemented in 2000 (Biggs & Potgieter 1999).

FAUNA

When the Sabi Game Reserve (the forerunner of the KNP) was proclaimed in 1898, the faunal populations were decimated by excessive hunting and the rinderpest pan-zootic which swept through southern Africa in 1896 and 1897. Some species (such as elephant and white rhino) were even locally extinct (Stevenson-Hamilton, 1903a & b).

The following is a summary of the faunal diversity of KNP.

Fish:	53 species - includes 2 exotic carp species (Pienaar 1978; Zambatis 1997b)
Birds:	505 species (Newman 1980; Sinclair & Whyte 1991; Whyte & Zambatis 1997)
Amphibians:	35 species (Pienaar *et al.* 1976; Zambatis 1997a)
Reptiles:	120 species (Pienaar *et al.* 1978; Zambatis 1997d)
Mammals:	147 species (Pienaar *et al.* 1987; Zambatis 1997c) including thefollowing:

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Order	No. of Species	
Insectivora (shrews etc)	9	
Chiroptera (bats)	43	
Primates	5	
Carnivora	27	
Perissodactyla	3	(2 rhinos, 1 zebra)
Hyracoidea (dassies)	2	
Tubulidentata (Aardvark)	1	
Artiodactyla	25	(2 pigs, 1 hippo, 22 antelopes)
Pholidota (pangolin)	1	
Rodentia (rodents)	25	
Lagomorpha (hares)	3	
Macroscelidae (elephant shrews)	3	

The most recent estimates of the numbers of mammals are as follows:

Lion:	1 500	Leopard:	1 000
Cheetah:	200	Wild dog:	350
Spotted hyaena:	2 000	Elephant:	9 152
White rhinoceros:	3 000	Black rhinoceros:	300
Burchell's zebra:	32 000	Hippopotamus:	3 000
Warthog:	1 500	Giraffe:	5 000
Buffalo:	21 095	Eland:	500
Roan antelope:	50	Sable antelope:	880
Greater kudu:	3 500	Nyala:	>300
Bushbuck:	>500	Waterbuck:	1 500
Reedbuck:	300	Mountain reedbuck:	150
Blue wildebeest:	14 000	Tsessebe	360
Impala:	>150 000		

Insect species have as yet not been comprehensively studied (Braack 1991), though an earlier survey of butterflies yielded 219 species (Kloppers & van Son 1978).

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CHAPTER 3: BAOBABS AND ELEPHANTS IN THE KRUGER NATIONAL PARK.

INTRODUCTION

This chapter is based on the information presented in a paper by Whyte *et al.* (1999), and a report by Whyte *et al.* (1996).

Some of the negative impacts of high densities of elephants on boababs elsewhere in Africa have been documented. Leuthold (1977) reported that as a result of elephant exploitation in Tsavo National Park (Kenya) the boababs had almost been exterminated. Once abundant, too few were recorded to include in his analysis of elephant damage to the Parks' tree species. A decline was also recorded in baobabs in Ruaha National Park (Tanzania) between 1976 and 1982. This decline was halted by 1989 which was attributed to by the poaching of most of the Park's elephant bulls (Barnes *et al.* 1994). In Mana Pools National Park, 29% of a sample of 124 baobabs was killed by elephants between 1984 and 1988 (Swanepoel 1993a; Swanepoel & Swanepoel 1986). These impacts have been associated with elephant populations considered to be at high densities, but in KNP there is some evidence that even at the relatively low densities at which the elephant population has been held, they may have been partly responsible for a gradual decline in the baobab population.

In Africa the baobab is unique and unmistakable. Carbon dating has put larger specimens at over 3 000 years old (Coates Palgrave 1977). He described the trees as "comparatively short (10 m to 15 m in height) but grotesquely fat – the boles in large specimens reaching 28 m in circumference", and because of its unique characteristics, they are "surrounded by a wealth of African legend and superstition (e.g. that God had planted the tree upside down)". Trunks of older trees are gnarled, dented and grooved. They are also often hollow and these characteristics lend themselves to use by a variety of species for roosting and nesting. The only known natural nesting sites of both the Mottled spinetail *Telecanthura ussheri* and Böhm's spinetail *Neafrapus boehmi* are in hollow baobabs (Harwin 1989; Maclean 1993; Sinclair & Whyte 1991). Other species which favour baobabs for nesting are the northern race of the Cape parrot *Poicephalus robustus suahelicus* and the Mosque swallow *Hirundo senegalensis* (Maclean 1993). As other species are dependent upon boababs, these trees are considered a "keystone" species, and as such must form an important component of KNP's biodiversity maintenance policy (Whyte *et al.* 1997).

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The objective of the original report (Whyte *et al.* 1996) was to examine the demography of the baobab population in KNP with a longer-term objective of establishing a monitoring programme through which the causes of mortality of these trees might be identified.

Age determination of baobabs has proved problematic. Guy (1970) found that in known age baobabs of up to 127 cm in diameter core samples yielded estimates of age accurate to within two per cent. He did not assess the value of the technique for larger trees. In 1980/81 Gertenbach (pers. comm.[1]) extracted cores from baobab trees in KNP in an effort to relate growth rings to climatic (rainfall) cycles. However, the trunks' centres were too porous and sections could not be obtained by means of a core. The thin outer layers of the trunks were also too thin for use in correlations of growth layers with long-term rainfall patterns. The age that baobabs may potentially achieve is thus not known. Measures of the girth of these trees are flawed as an age determination technique, as these trees are known to contract as a result of moisture loss during droughts (Guy 1970). For instance a baobab tree measured by David Livingstone in 1853 and by Guy in 1966 had shrunk by some 11% (Guy 1970).

Nothing is known of long term recruitment and mortality rates for baobabs. Nel (1988) estimated the Kruger National Park baobab population at 20 000 trees, but was of the opinion (Nel pers. comm.) that "over the past decade" (1986 -1996) more than 1 000 of these trees had died. Between 1993 and 1995 alone, 151 freshly dead baobabs were recorded during aerial censuses (Whyte & Wood 1994b; 1995). Although it is known that drought alone can be responsible for baobab mortality, it is thought that baobabs' susceptibility to drought is exacerbated through bark stripping by elephants which may increase moisture loss.

STUDY AREAS

This study focused on three areas which can all be considered high-density baobab areas but which have been subjected to different elephant densities over different periods of time. Two of these areas occur in the northern KNP (Figure 5) while the third (Messina Nature Reserve) falls outside the KNP about 120 km to the west. These three areas are:

[1] Dr W.P.D. Gertenbach, Department of Wildlife Management, Kruger National Park.

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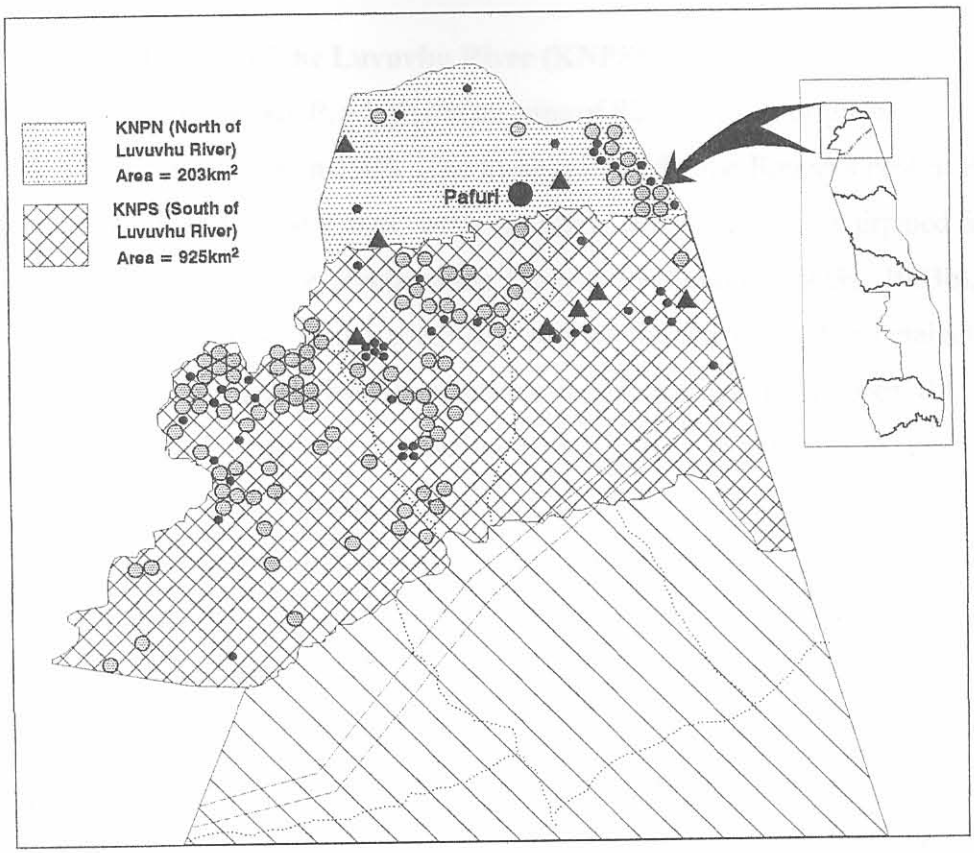


Figure 5: The Kruger National Park study areas. Localities of baobabs that had died are shown by: ◎ in 1993 (n = 95), • in 1994 (n = 48), and ▲ in 1994 (n = 48).

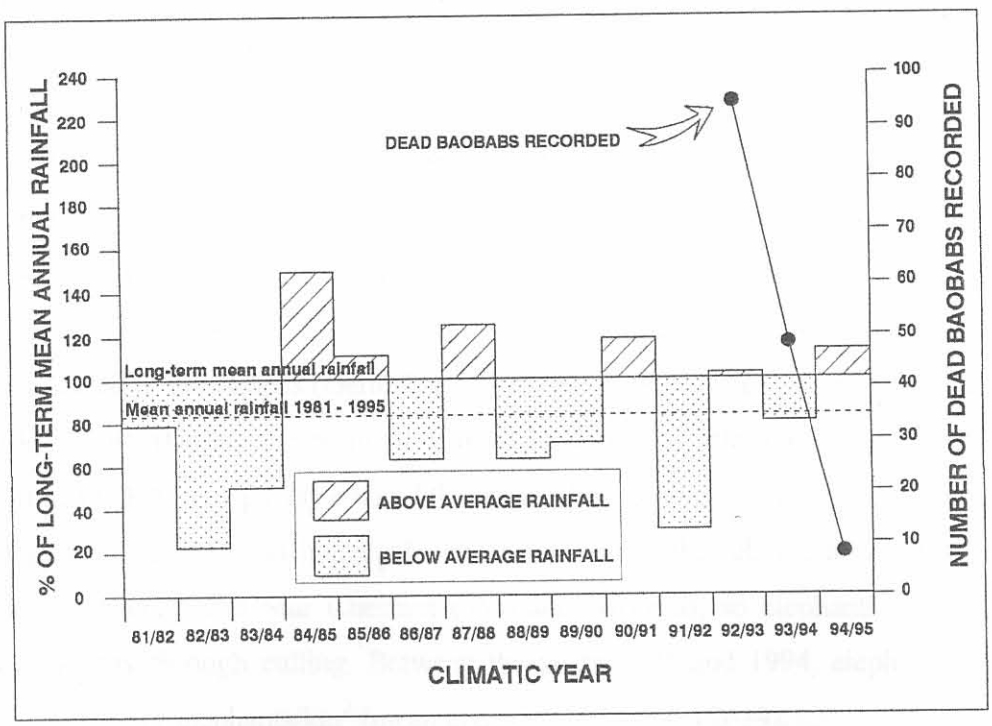


Figure 6: Rainfall measured at Pafuri between 1981 and 1995 and dead baobabs recorded between 1993 and 1995.

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Kruger National Park south of the Luvuvhu River (KNPS)

The study area in this part of KNP, which has an area of 925 km^2, was originally proclaimed as the Shingwedzi Game Reserve in 1903. The mean rainfall for the Ranger's post at Pafuri is 420 mm and it lies at an altitude of 250 m above sea level. Elephants were extirpated from the area at some unknown time before proclamation (Stevenson-Hamilton 1903a; 1903b), but in 1905 elephant spoor was found in the south-east part of this area near the Letaba/Olifants confluence and it was estimated that 10 elephants then occurred in the area (Stevenson-Hamilton 1905). In 1926 this area was included in the KNP upon its proclamation as a national park. In 1931 elephants started to recolonise the baobab area of the KNP according to ranger's reports (Stevenson-Hamilton 1931). The elephant population of the area subsequently increased until 1967 when culling campaigns were initiated to maintain the total population of KNP at around 7 000 individuals. Between the years 1985 and 1994, elephant densities ranged from 0.14 to 0.81 elephants/km^2 (mean and S.E. = 0.356 ± 0.2001). The KNP landscapes (Gertenbach 1983) of this study area are nos. 15, 16, 23, 25, 26, 27, 28, 32 and 34 (See Figure 4). Baobabs occur in all of these landscapes. Unfortunately, cull records are inadequate to allow the designation of numbers of elephants culled to each of these areas.

Kruger National Park north of the Luvuvhu River (KNPN)

This area of 203 km^2 did not initially form part of the KNP at its proclamation in 1926, but was only added in 1969. Rainfall and altitude are similar to those of the KNPS. It is unlikely that any elephants have been present in the area since the decline of the town Schoemansdal, described as the elephant hunters' Mecca, which thrived between 1846 and 1867 (Pienaar 1990; see Chapter 4). It is likely that by this time and probably from even before, these hunters were hunting elephants to the north of the Limpopo River in Zimbabwe (then Rhodesia) and Mozambique. The KNP landscapes (Gertenbach 1983) of this study area are nos. 16, 25, 26, 27 and 28 (See Figure 4). Baobabs occur in all of these landscapes. After the proclamation of the KNPN as part of the KNP, elephants entered the area in low numbers. It was perceived to be an area of ecological sensitivity and botanical importance due to the relative abundance of rare trees such as the baobab and Star Chestnut (*Sterculia rogersii*), so elephants were kept at relatively low density through culling. Between the years 1985 and 1994, elephant densities ranged from 0.03 to 0.77 elephants/km^2 (mean and S.E. = 0.305 ± 0.2639).

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Messina Nature Reserve (MNR)

The MNR was proclaimed in 1976 as a baobab reserve. It is 4 471 hectares in extent and is situated 5 km south of the town of Messina in the Northern Province of South Africa. It lies at an altitude of 600 m above sea level and the mean annual rainfall is 299 mm. As with the KNPN area, it is unlikely that any elephants have been present in the area, at least since the establishment of the town of Schoemansdal in 1846.

This reserve falls within Acocks' (1988) Veld Type Number 15 (Mopaniveld).

METHODS

Baobab data

The KNP data used to indicate size classes of the trees come from the studies of Whyte *et al.* (1996) and from Nel (1988). The MNR data were from Steyn (1990).

Baobabs were located while travelling along roads in a vehicle. In KNP distribution is often clustered and many trees can be accessed on foot. In the clusters sampled, all trees were examined. While travelling in the vehicle or moving between trees on foot, a diligent search for smaller trees was conducted by slow movement and careful scanning, but the obscure nature of small baobabs probably resulted in under-sampling of this class. Data were obtained from all trees found. Data were recorded from 220 boababs in KNPN and from 204 boababs in KNPS in July 1995 and January 1996. For each of these (alive and dead) girth was measured at breast height (GBH) to the nearest cm. A photograph was taken of each tree and its position was plotted using a Global Positioning System (GPS) to allow for certain recognition on subsequent surveys.

During the 1993, 1994 and 1995 aerial (helicopter) censuses of the KNP elephant and buffalo populations (Whyte & Wood 1994a; 1994b; 1995), the numbers and approximate localities of dead baobabs which had died within the past year, were recorded on the census maps. (Such trees are easy to recognise as within a few months of dying, they collapse into a heap of pulp which is initially a fairly yellow colour. The pulp of trees dead for a longer period turns grey).

Elephant damage

Damage to bark of baobabs remains visible for a very long time. Some early European visitors to the KNP area carved their names with dates on these trees as far back as 1890 and are still

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clearly after 110 years. If elephants were utilising baobabs 100 or even 200 years or more ago, it could be expected that the scars would still be clearly visible. Nel (1988) differentiated between "old" and "new" elephant damage to the bark of baobabs. Old damage was that which he could recognise as elephant damage, but which had healed to a point where it had regained the colour and texture of old bark. He estimated that this process took about seven years.

Whyte *et al.* (1996) only examined fresh damage in the KNPN and KNPS regions of the KNP as their study was specifically aimed at acquiring a better understanding of the factors affecting baobab mortality. "Old" damage which had healed completely was assumed to no longer be a factor affecting the trees' chances of survival, and an assessment of the severity of "new" elephant damage only was conducted.

The amount of damage was recorded as either none, slight (some utilization but shallow and tree not ring-barked), moderate (utilization shallow but tree ring-barked), severe (tree ring-barked: utilization affects the shape of the trunk), very severe (utilization dramatically affects the shape of the trunk).

RESULTS

Dead boababs

Nel (1988) estimated KNP's baobab population at around 20 000 individuals, and is of the opinion (pers. comm.) that in the 15 years up to 1995, more than 1 000 (5%) of this initial population had died. The majority of the mortality occurred before 1993 (which was the last of the serious drought years) but unfortunately the numbers and localities of these dead trees were not recorded. However, between 1993 and 1995, a further 151 dead trees were recorded of which 95, 48 and eight were noted in these three years respectively (Whyte & Wood 1994a; 1994b; 1995). No fresh mortalities were recorded in 1996. Mortality therefore declined from 0.48% in 1993 to 0.24% in 1994, 0.04% in 1995 and 0% in 1996 which may be related to the higher rainfall which fell towards the end of the period (Figure 6). The localities of the dead trees are shown in Figure 5.

Of the 220 baobabs examined in KNPN during the most recent ground survey, four (2.0%) were dead, while in KNPS , 11 (5.4%) of the 204 trees examined were dead. The difference in these proportions was not significant ($\chi^2 = 2.98$; $p > 0,1$). No dead trees were recorded in MNR.

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Population structure

The size structure of the baobab populations (Figure 7) from the three areas differed significantly (Kolmogorov-Smirnov 2-sample polynomial tests for KNPS vs KNPN ($p = 0.0002$), for KNPN vs MNR ($p = 0.001$) and for KNPS vs MNR ($p = 0.0002$). In the MNR a very high proportion (50%) of trees in the sample had a circumference of < one metre. Similarly the KNPN sample had a high proportion of younger trees though with a much smaller proportion of trees in the first age class than in the MNR.

There were clearly more trees in the middle size classes (4 - 9m circumference) in all three areas, which suggests that for some period in the past, recruitment and/or survival rates were better than at present (Figure 7).

Elephant damage

As there are no elephants in the MNR, no damage was recorded. In the KNPN, 169 (76.8%) of the 220 trees sampled were either undamaged or showed only slight damage with 51 (23.2%) trees in the more severely damaged classes (Figure 8). In the KNPS however, a significantly ($\chi^2 = 20.86$; $p < 0.001$) higher proportion of trees were recorded in the more severely damaged classes as 113 and 91 of the 204 sampled were recorded in these two categories respectively.

DISCUSSION

Population structure

The distribution of the size classes in the MNR sample is indicative of a very healthy population with a high proportion of young trees and decreasing proportions into the larger (older) size classes. In the KNPN, the size class distribution suggests that the age structure of this population also favours higher proportions of younger trees than in the larger size classes. The KNPS sample however, shows an opposite trend, with a reduced proportion of trees in the younger classes (< 6m). For the 30 years prior to the present study, the KNPS supported a higher density of elephants than the KNPN. The pattern recorded in these three areas conforms closely to the results of three surveys conducted in the Ruaha National Park (Barnes 1980, 1985; Barnes *et al* 1994). Barnes *et al.* (1994) reporting on the three surveys wrote that *"The 1976 size distribution indicated a healthy population with more young than old trees. By 1982 there*

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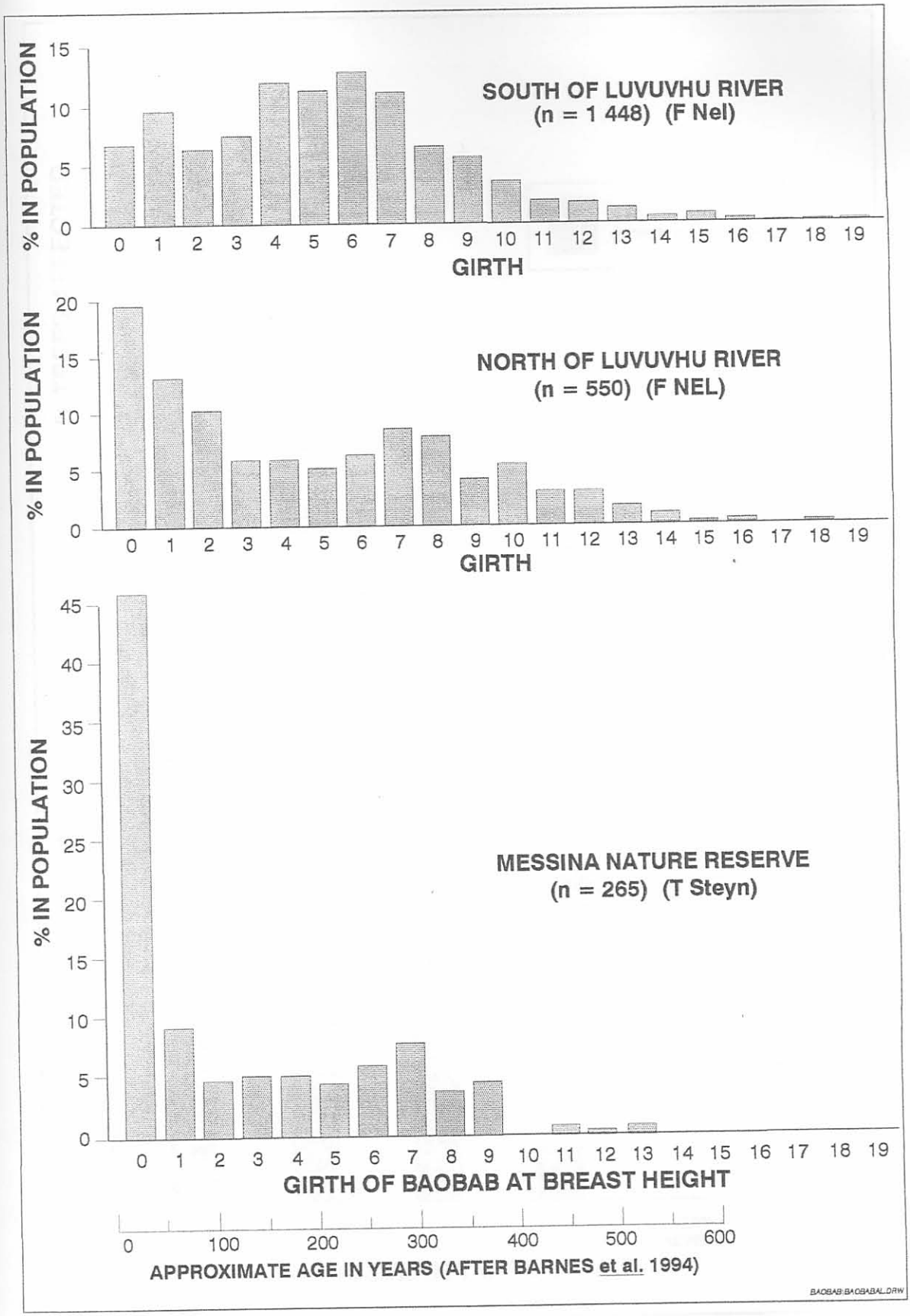


Figure 7: Size structure of the baobab populations of the three study areas and the age estimation method of Barnes *et al.* (1994).

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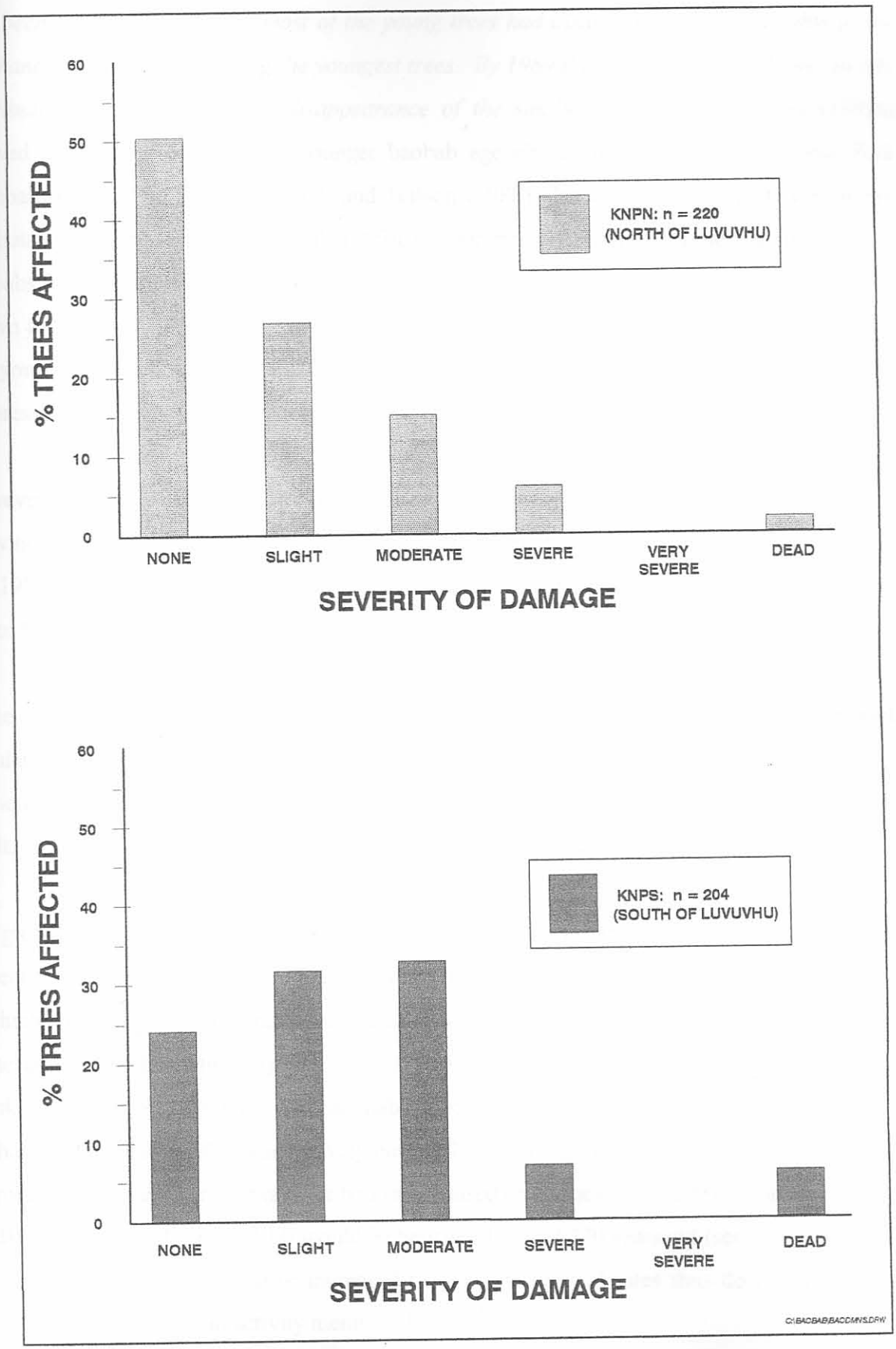


Figure 8: Classes of elephant damage to baobabs in the two study areas (KNPN and KNPS) of the Kruger National Park.

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had been a dramatic change: most of the young trees had disappeared. This was due to the elephants' preference for eating the youngest trees. By 1989 there was a further change in size distribution, with the complete disappearance of the smallest class". Swanepoel (1993a) showed a similar decline in the younger baobab age classes in Mana Pools National Park (Zimbabwe) between 1984 and 1988 and Wilson (1988) also reported a lack of recruitment attributable to elephants in certain other African countries. Differences in the age structures of boababs in the three study areas may thus be the consequence of elephant damage which was shown to be significantly greater in KNPS than KNPN. Though the complete disappearance of the younger age classes has not occurred in KNPS, it is clear that recruitment is being suppressed and that a similar process is now in an earlier stage in KNPN.

However, in spite of the disappearance of the youngest size class, Barnes *et al.* (1994) could show no significant difference between the population structures recorded in Ruaha in the 1982 and 1989 surveys. They attributed this to a 60% decline in the Park's elephant bull population due to heavy poaching between 1977 and 1984.

Barnes' (1980) model of elephant predation on baobabs suggests that while an elephant population is static (not increasing), a baobab population will decline but not to the point of extinction, but that when the elephant population is increasing, extinction would be the end result.

The greater proportion of trees in the middle size classes (4 m to 9 m circumference) which are evident in the samples from all three of the study areas (Figure 7) suggest of a period in the past in which recruitment/survival rates were relatively high. This may be related to human presence in the area in the late Stone Age by the San people (up to 300 AD) and thereafter by Bantu (Cooke 1969; Eloff 1990a). Human habitation could have discouraged the presence of elephants, particularly if they had actively hunted them (see Chapter 4). This in turn could have improved recruitment/survival rates of baobabs. Based on Barnes *et al.* (1994) baobabs in these middle size classes (4 - 9 m GBH) would be between 170 and 370 years old (see Figure 7). The ages of the trees in the period of increased recruitment/survival rates thus do not match the periods of increased human activity mentioned above.

The method of Barnes *et al.* (1994) implies a linear relationship between age and GBH, while Swanepoel (1993b) showed that, at least in the Zambezi Valley, this is not the case and that

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growth rate varies between trees of differing GBH. Swart (1963) estimated a baobab with a girth of 14.36 m as to be 900 – 1100 years old, while the method of Barnes placed this tree in the 550 - 600 year old class.

The age determination techniques for baobabs (using GBH) are thus not consistent, and the suggestion that man's impact on elephants in turn influenced baobab recruitment/survival rates can not be supported.

Elephant damage

Pienaar (In litt.[2]) suggested that baobabs heal almost entirely, new bark being laid down *"under the outer layer of fibrous woody pulp. Within months to a year or so these trees will boast an entirely new and smooth layer of bark over their gnarled trunks when the outer fibrous debris sloughs away, and all the evidence of the debarking that remains is a ring-like scar of thickened bark at a height of 2.5 to 3 metres from ground level".* Nel (1988) however suggested that it took around seven years for the bark of a baobab to heal after being stripped by elephants. Either way, this means that if damage is older than seven years, it is not possible to estimate when such bark stripping may have occurred. While a considerable proportion of the boababs in KNP showed evidence of "old" bark stripping (Nel 1988), the fact that no estimate of the age of the damage is possible means that this can not be used as an indication of the historical presence of elephants.

CONCLUSIONS

The majority of known baobab mortalities in KNP occurred between 1981 and 1994 during the extended dry cycle (drought) to which the Lowveld was subjected. Some trees are known to have died with very little or no visible elephant damage (Scott Ronaldson, pers. comm.[3]). Drought is clearly one of the major agents of mortality for baobabs. However, baobabs damaged (debarked) by elephants may have an increased vulnerability to drought due to increased moisture loss from the stem areas left unprotected.

It is known that elephants at extremely high densities are capable of major impacts on baobab

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[2] Dr U. de V. Pienaar, Retired Chief Director SANP, Stilbaai.
[3] Mr G. Scott Ronaldson, Senior Ranger, Mahlangene, Kruger National Park.

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populations. The rapid disappearance of these trees from Tsavo East National Park in Kenya (Leuthold 1977) is one example, and the disappearance of the youngest size classes in Ruaha (Barnes *et al* 1994) is another. In the absence of elephants (as in MNR), recruitment rates can be very high, while in KNPN the exclusion of elephants for more than 100 years has resulted in a recruiting population. Elephant damage is much less prevalent in KNPN than in KNPS. In the KNPS area where elephants have been present for longest, recruitment rates are lowest in spite of the elephant population having being maintained at a relatively low level through culling.

While it is as yet unclear whether baobab recruitment rates at current elephant densities are sufficient to maintain a stable population, it is likely that an increasing elephant population would have greater impacts (Barnes 1980). It seems reasonable to expect that due to their current confinement in KNP, elephant ranging or feeding patterns will have changed. This may have resulted in an increased pressure on baobabs. However, it seems more likely that if at any time in the past 500 to 1000 years elephant densities were significantly higher than those current in KNP, baobabs would be unlikely to occur at their current densities. Is this evidence that elephants have been at a lower density for an extended period? Other evidence presented in the Chapter 4 also supports this postulation.

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CHAPTER 4: THE PRE-MANAGEMENT ERA (HISTORY OF THE KRUGER NATIONAL PARK ELEPHANT POPULATION UP TO 1966)

INTRODUCTION

Various reports have been written on the history of elephants in South Africa (Bryden 1903; Ebedes *et al.* 1991; Hall-Martin 1992). van Wyk & Fairall (1969), gave a brief summary of the history of the elephants in Kruger National Park (KNP) but as yet no specific investigation into the history of the population of the Lowveld area of RSA (including the KNP) has been undertaken. This chapter gives a detailed history of the KNP population and has been divided into three phases - prior to the arrival of the Europeans, post arrival of the Europeans, and post proclamation of the area as a game reserve/national park up to the time that elephant management was initiated.

Earlier authors have suggested that in the past elephants occurred in the KNP area in considerable numbers (Rowland-Jones 1955; Pienaar 1990; 1996), but the interpretation of all of the information gained for this study suggest that numbers of elephants in this part of Africa have perhaps always been low, though the reasons for this are somewhat obscure.

MATERIALS AND METHODS

Data and information presented are entirely from a literature survey which included books, scientific literature, unpublished reports, annual reports from KNP, and diaries of earlier Wardens and Rangers.

Quotes in italics were translated by me from Afrikaans to English.

HISTORY PRIOR TO THE ARRIVAL OF EUROPEANS

Prehistory

Of the many forms of Proboscidae which evolved world wide, not all have been recorded in Africa (Shoshani 1991). Eloff (1990a) speculated that *"other types of elephants"* could have occurred in the KNP area as recently as 200 000 years ago, but there are no fossil records to substantiate this.

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The San (Bushman) era

Stone artifacts found over most of the KNP show that people were living in the KNP area during the Early, Middle and Later Stone Ages between 7 000 BC to 300 AD (Eloff 1990a; 1990b). The San (Bushmen), whose characteristic rock paintings are still visible in rock shelters in both the south-western and northern areas of the KNP, were associated with the latter part of the Late Stone Age between 7 000 BC and 300 AD (Cooke 1969). Elephants may have occurred in the area as there are three known paintings in rock shelters in the KNP. One of these in a rock shelter along the Nwatindlopfu River shows a group of five of these animals (English 1990). It may be expected that a large and dangerous animal like the elephant which, if it could be killed, would feature prominently in Bushman folk lore. Woodhouse (1992, 1996) suggested that elephants were a popular theme for paintings as they "provided a lot of meat and were associated with water and rain which the Bushmen artists were keen to influence".

It is now also widely accepted that San paintings depict the spiritual experiences of shamans (ritual specialists) during trances (states of altered consciousness) induced by ritual dances (Lewis-Williams 1996; Lewis-Williams & Dowson 1989). These authors suggest that San art was not narrative of their lifestyles nor "menus" representative of their diet, and that the incidence of different species in their art may not be reflective of their relative abundance. However, if elephants were popular elsewhere as artistic subjects (Lewis-Williams & Dowson 1989) and were "associated with water and rain which the Bushmen artists were keen to influence" (Woodhouse 1992, 1996), then it is perhaps still significant that they are such a rare feature of the San art in KNP. Of the 109 shelters with rock art located in the KNP thus far, there are only three paintings showing elephant. One other shelter with elephant paintings has been found in the Brondal area, some 30 kms to the west of the KNP between Nelspruit and White River (Bornman 1995). The relative scarcity of elephants in the rock art of the KNP and surrounding area suggests that these animals were rare during the San era.

The arrival of the Bantu

During the period ca. 200 to 500 AD immigrants with small herds of domestic stock, ceramic traditions and a knowledge of iron working penetrated the area (Joubert 1986). From this era, Plug (1984; 1989) reported on archaeozoological remains from 12 sites in the KNP. Only one of these

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sites (Tsh 1 on the Mutlumuvi River near Tshokwane) contained elephant remains. The date for this site was estimated at about 510 AD. This scarcity of elephant remains may however bare no relation to the numbers of elephants. Usually, only the meat and tusks would have been carried back to dwellings as the other remains (bones and hides) would have been too heavy, and have no known cultural value to these people.

The impacts that any of these people may have had on whatever elephants populated the area during those times is entirely unknown. An archaeological site known as Schroda, situated near the Limpopo River approximately 200 km to the west of the KNP, rendered "large quantities" of ivory in conjunction with cowries, suggesting a participation in the ivory trade (Plug & Voigt 1985). The ages of the remains at Schroda were estimated as originating between the eighth and ninth centuries by ^{14}C dating. These authors concluded that the presence of glass beads at this site strengthened the evidence for their link with the coastal trade during the eighth century.

Between circa 900 and 1220 AD trade in gold and ivory became established on an increasing scale between the indigenous people inhabiting the Limpopo River area and the Islamic empire, and centres of trade became established at Bambandyanalo and Mapungubwe. The "golden age" of Mapungubwe lasted until circa 1290, but the virtual absence of ivory from Mapungubwe combined with the presence of gold in the uppermost levels (of the excavation) suggests that by the 12th century, the trade had switched to gold and the trade routes had moved farther north leaving the Limpopo valley a virtual backwater (Plug & Voigt 1985). Could this switch to gold, the lack of ivory in the archaeological sites, and the shift in trade routes perhaps have been due to a paucity of elephants?

Great Zimbabwe then grew in importance as a centre of trade and culture (Plug & Voigt 1985). This era lasted for approximately 100 years when, upon the decline of Great Zimbabwe in 1420, some of the people moved south and established themselves in the northern KNP at Thula Mela, Makahane, Matjigwili (Mashikiri) and also in a chain of stone wall villages on hill tops from Thula Mela westwards towards Messina and beyond (Eloff 1966: Küsel 1992). These sites were inhabited from the 15th to the early 19th centuries. Another archaeological site (Sh 16 near Red Rocks in the Shingwedzi area) reported on by Plug (1984) also contained elephant remains.

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This site was dated at between AD 1500 - 1900.

The Portuguese established trade with south-east Africa in the early 1500's (Smith 1970). He wrote that in 1544 they (the Portuguese) "reported that 'great quantities' (of ivory) could be obtained at Delagoa Bay, but that by 1680 the English had bought up all the supplies reaching this port, so that there was 'virtually none left in the country'". Unfortunately, quantities of ivory were not given, and subjective statements like "great quantities" give no indication of how much ivory this may have been. Also, there is no indication of where the ivory might have come from. Some of this ivory may have come from the KNP area, as Delagoa Bay was the closest port.

Alpers (1975) was of the opinion that the technology of elephant hunting only became dominated by firearms from the middle of the nineteenth century, but that there was evidence of their use a century before this in Mozambique. While it is known that prior to this the indigenous Africans were capable of killing elephants (Alpers 1975), it is not known what sort of impacts they may have had on the elephant populations. According to Alpers, the methods used were to dig deep pits, plunging heavy spears between the shoulder blades from tree-perches, and severing the tendons in the elephant's leg using a wide-edged axe. It would seem unlikely that these means that they had at their disposal would allow them to significantly reduce elephant population numbers, but it may be that the mere presence of humans capable of hunting elephants was enough to keep their numbers low. Whyte *et al.* (1998; see Chapter 6) estimated that the selective removal of as few as between 3-6% of the population could be sufficient to stabilise it.

There is some evidence from the population structure of baobab trees in the northern KNP that people may have had some influence on numbers of elephant (Whyte *et al.* 1996; see Chapter 3). Elephant densities were possibly low at this time as a result of this human presence and their trade in gold and ivory, which in turn could have resulted in an increased survival of baobabs (Whyte *et al.* 1996). This conclusion was drawn from the fact that damage to bark of baobabs remains visible for a very long time. Some early European visitors who were in the KNP area carved their names with dates on these trees. On one such baobab in the Tsumaneni Spruit near Bangu in the KNP, is carved: "BRISCOE 1890". This carving, now 110 years old, is still as clearly visible. If elephants

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were utilising baobabs 100 or even 200 years or more ago, it could be expected that the scars would still be clearly visible. Yet 50% of the trees in the northern KNP show no damage at all, and the damage to those that have been utilised is reasonably new.

Another possible point of significance in the discussion of the history of elephants in KNP is the wide diversity of plant taxa still extant in the KNP. Elephants are known to eliminate some plant species in areas where they occur at high densities for extended periods of time (e.g. Leuthold 1977; Page 1999). According to Waithaka (pers.comm.[1]), Amboseli National Park in Kenya has lost more than 50% of the plant species that occurred there due to the high densities of elephants. The near eradication of baobabs from Tsavo National Park in a short period of time (Leuthold 1977) and the fact that they are still abundant in northern KNP (the southern tip of their range in Africa) indicates that in KNP, elephants could never have achieved the densites they did in Tsavo. The herbarium list in Skukuza records 1 982 taxa for the KNP (Zambatis 1997e) and there is no evidence of any species lost from KNP, but the eradication of the stands of aloes *(Aloe marlothi)* from the Doispane and Sabie River areas of the KNP in 1959 (see Biologiese Afdeling (1959) below) is evidence of their potential impacts on species diversity even at low densities. This plant diversity of KNP is thus suggestive of an area with a long history of low densities of elephants.

Post colonisation (arrival of the Europeans)

The first writings on the area now known as the KNP come from the diaries of Francois de Cuiper. In 1721 the Dutch "Verenigde Oos-Indiese Compagnie" (V.O.C.) established a base in Delagoa Bay through which it was hoped to establish an "ivory and gold trade with Monomotapa" (Punt 1990). In 1725 de Cuiper and his party of 31 undertook an expedition into the interior to reconnoitre a trade route to Zimbabwe. They marched to the north-west to the Matola River which they named the "Olifants" because "the Matola area was the home of large herds of elephants" (Punt 1990). This is only about 70 km from the present KNP boundary and is the only mention made of elephants on this expedition. These men penetrated the extreme south-eastern region of the KNP area which, according to his account, was well populated by black people as they passed through several villages situated about one day's march apart. They enquired of the road to "Ciremandelle" (Phalaborwa) and Thowelle (Zimbabwe) from these people and were informed that

[1] Dr. J. Waithaka, Kenya Wildlife Service, Nairobi, Kenya.

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at Ciremandelle there was little gold but much copper and that at Simangale in the Thowelle area, there was much gold, copper and ivory (Punt 1990). However, due to the hostile attitude of these people, which ended in a skirmish, the party was forced to retreat and return to Delagoa Bay.

It is of interest that the immediate interior, including the KNP area, were not perceived by these indigenous people as an "ivory area" but that ivory was plentiful in Zimbabwe. This suggests a low density of elephants in the KNP area at that time.

Much later, in 1838, Louis Trichardt crossed the KNP area on his trek from the Soutpansberg to Lorenco Marques (Preller 1917). The only mention of elephants in Trichardt's diaries was of a hunt in May 1837 in the Soutpansberg area, and of an unsuccessful hunt on 28 April 1838, after their arrival in Lorenco Marques. Neither of these hunts occurred in the KNP area and no other mention was made of these animals. Had opportunity presented itself, they would almost certainly have hunted the elephants and he would have recorded the incidents in his diaries. It may be assumed that elephants were uncommon there at that time also.

Joâo Albasini was the first white settler in the KNP area. Based on Pienaar (1990) Albasini arrived in Delagoa Bay in 1831 and established himself as a hunter and trader in Mozambique and the eastern Transvaal. Initially he traded ivory from Lorenco Marques and in 1841 he formed a company with nine others, who would, "... by common agreement ... shoot elephants in the territories neighbouring this garrison ... ". The company's only objective was to "... increase the ivory trade which is today so diminished by the Negroes of the interior...". Twenty-five people were employed solely to shoot elephants. It is not known how successful this venture was or where these elephants were to be shot, but six months later Albasini parted ways with the Company. He then established himself in the Phabeni area in the southern KNP where he reputedly also traded in, among other things, ivory. After two years there he abandoned the store and moved to Ohrigstad, Lydenburg and finally in 1853 to the Soutpansberg in the northern Transvaal. Although it is nowhere stated as such, the outcome of all of these ventures hint of an elephant population at too low a density to sustain viable hunting and trade.

Rowland-Jones (1955) was not entirely in agreement with this. In his own words:

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"I have, for many years, interested myself in the gradual rehabilitation of the elephant in the Park, and I have taken every opportunity of trying to ascertain the position as it was at the beginning of the century.

"In the North, European hunters and recruiters and old natives born in that country all confirm that no elephant were to be found and the ivory hunters had left the district long before that. Col. Stevenson-Hamilton and his rangers found the same thing to be the case in the old Sabie Game Reserve - the elephant had been annihilated long before their arrival in the Lowveld.

"The reason for this is not hard to find. One Albasini, a Portuguese trader, appointed himself head of the Shangaan tribe and setting up his headquarters on the Sabie River sent out his hunters to scour the country for ivory. Their methods were so effective that in time no elephant survived in the old Sabie Game Reserve, so Albasini had to move to new pastures. The whole Tribe migrated to the Zoutpansberg district, setting up their headquarters in the Groot Spelonken from where the hunters moved down into the Lowveld and combed the countryside from the Klein Letaba to the Limpopo even penetrating far into Portuguese Territory. This locust-like invasion finally reduced this area to the same state as the Sabie.

"One area of the Park, the portion between the Letaba and the Olifants rivers lying approximately half-way between Pretorius Kop and Spelonken appears to have missed this devastation and a small nucleus of elephant survived in this local Mesopotamia.

"In 1910 the Willis Brothers trekked through Punda Maria to Malonga and the first elephant spoor which they found was 70 miles east of the Limpopo, nearly at the Great Save River, so the devastation had been pretty complete".

In 1853 the town Schoemansdal near the Soutpansberg was described as the elephant hunters' Mecca which thrived between 1846 and 1867 (Pienaar 1990). When German traveller Carl Mauch visited that area in 1871 he wrote, "... 25 years ago (1846?) the killing of elephants was very productive and the profit enormous ..." but by 1871, "... elephant hunting was no longer practical ...

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too expensive" (Burke 1969).

By 1897 Millais (1899), when visiting the Schoemansdal area, wrote, "Two days ago we caught up with the De Mervelles, the Basadanotes, and Daniel Erasmus, who are among the few Dutch hunters who now trek every year from the Transvaal to the northern hunting-grounds; for now that the elephants are nearly gone, hunting affords but a poor and precarious mode of existence, and all those poor fellows are, like Van Staden, on the verge of beggary".

Bernard Lotrie was one of the more active hunters of the time in Schoemansdal (Moerschell 1912) who fell upon hard times on the collapse of elephant hunting. As with the other hunters of the time it is unclear where he conducted his hunts. Pienaar (1990) concluded that it was mainly to the north in Zimbabwe and Mozambique. There is evidence however, that he had been in the KNP area from a carving in a baobab tree near Malonga Fountain which reads, *"B L 60"* which may be construed as "Bernard Lotrie 1860" (Pienaar 1990). From what has been quoted above, it is certain that by that time (and probably for many years before) not many elephants would have been present in the area, these hunters were shooting their elephants well to the north of the Limpopo River.

Regular hunting parties started to exploit the KNP area only from about 1870. Elephants still apparently occurred in the KNP area around 1880, but by 1896 these were no longer to be found there. In this regard Vaughn Kirby (1896) wrote, "I can well remember how 14 years ago the eastern portion of the Transvaal was a perfect paradise for big game of all descriptions - elephant, rhinoceros, hippopotami, buffalo, giraffe, roan and sable antelope, and in fact all the species of antelope peculiar to those regions. Now, alas! We speak of all of these animals, with the exception of giraffe and sable antelope, as we do of the deinotherium, megatherium and the dodo - things that have been". In this text he also wrote, "As lately as five years ago there were elephants on the Timbavati, a herd of 50 head being encountered by some boer hunters. They came from the extensive reed beds at the junction of the Letaba and Oliphants *(sic)* rivers, though they still exist in the dense bush on the slopes of the Libombo *(sic)"*.

Sandeman (1880) visited the KNP area to the south of the Sabie River in 1878 but made no mention at all of elephants.

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Glynn (undated), one of the few Lowveld pioneers who wrote of his experiences during the period 1873 - 1925, hunted extensively in the region, but speaks only of elephant hunting along the Pungwe River (much further to north in Mozambique). This suggests that elephants were already extremely scarce during that time.

In his chronicle of the decline of the elephant populations of southern Africa, Bryden (1903) gives specific accounts of many hunters and the areas in which they operated. He makes no mention at all of the Lowveld as an area where elephants were hunted.

"Bvekenya" Barnard hunted (poached) elephants from a base camp known as "Crooks' Corner" between 1910 and 1929 (Bulpin 1954). Crooks' Corner was situated just south of the Limpopo River in what is now part of KNP. No elephants occurred here however, and his hunting (and other poachers of the time) was conducted to the north in Rhodesia (Zimbabwe) and Mozambique.

It seems likely that the remnants of the population of elephants inhabiting what is now the KNP were shot to extinction between 1880 and 1896 by early European and Boer hunters, assisted by their African employees, none of whom kept records of their hunts.

There is thus no written record of the number of elephants which may have inhabited the KNP area prior to the arrival of Europeans, nor the amount of ivory which may have come from the area. It is perhaps significant that none of the hunters who left any record (e.g. Selous 1881; Finaughty 1916) hunted elephants in the KNP area. Those that did hunt there (Vaughn Kirby 1896; Glynn undated), did not shoot any elephants. This, along with the evidence from baobabs (Whyte *et al.* 1996; see Chapter 3), suggest that elephants occurred at relatively low densities, even during the Mapungubwe era around 900 AD.

Based on historical information from the San era through the Bantu colonisation era, the baobab record, and up until the arrival of literate white hunters, I conclude that elephants did not occur in large numbers in the KNP area. Elephants that did occur here at the time of the arrival of the white man and his firearms, were extirpated by them before the proclamation of the Sabie Game Reserve at the beginning of the century.

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Post proclamation as a game reserve in 1898

As an introduction to this era, the boundary changes to the KNP have been summarised in Table 3 and Figure 9. Although the Sabi Game Reserve was initially proclaimed in 1898, Colonel James Stevenson-Hamilton arrived as first resident Warden of the Sabi Game Reserve only in July 1902. His initial conclusion was that there were no elephants (Stevenson-Hamilton 1903a; 1903b). By 1905 spoor had been found of a few elephants near the confluence of the Letaba and Olifants rivers after which a steady increase in numbers was noted.

Table 3: Area and boundary changes to the Kruger National Park from 1898 to 1994.

Region (see Figure 9)	Name of area	Comments	Size (ha)	Total size of KNP (ha)
F	Sabie Game Reserve	Proclaimed as a game reserve in 1898	368 200	368 200
H+E	Private farms	Control of private farms was passed to KNP Warden in 1902/3	942 600	1 310 800
A+B+G	Shingwedzi Game Reserve	Proclaimed as a game reserve in 1903	851 300	2 162 100
I	Nsikazi west	Added to KNP in 1906	60 000	2 222 100
A	Pafuri	Excised in 1913	20 700	2 201 400
D	Letaba/Olifants (1)	Added in 1914	92 100	2 293 500
I	Nsikazi west	Excised in 1923	60 000	2 233 500
B+C+D+E+ F+G	Kruger National Park	Proclaimed as a National Park in 1926 (Area C added, Area H excised)	1 948 500	1 948 500
G	"Shingwedzi block"	Excised in 1969 in exchange for Area A (Pafuri)	20 700	1 948 500
A	Pafuri	Added in 1969 in exchange for Area G ("Shingwedzi block")	20 700	

The following accounts have been drawn from reports of the Park's Wardens and reflect the population growth since that time.

(Stevenson-Hamilton 1903a). "Elephants existed in fairly large numbers up to forty years ago in the Sabi Bush, but as there are no herds in any way adjacent I see no prospect of their returning to the Sabie Game Reserve".

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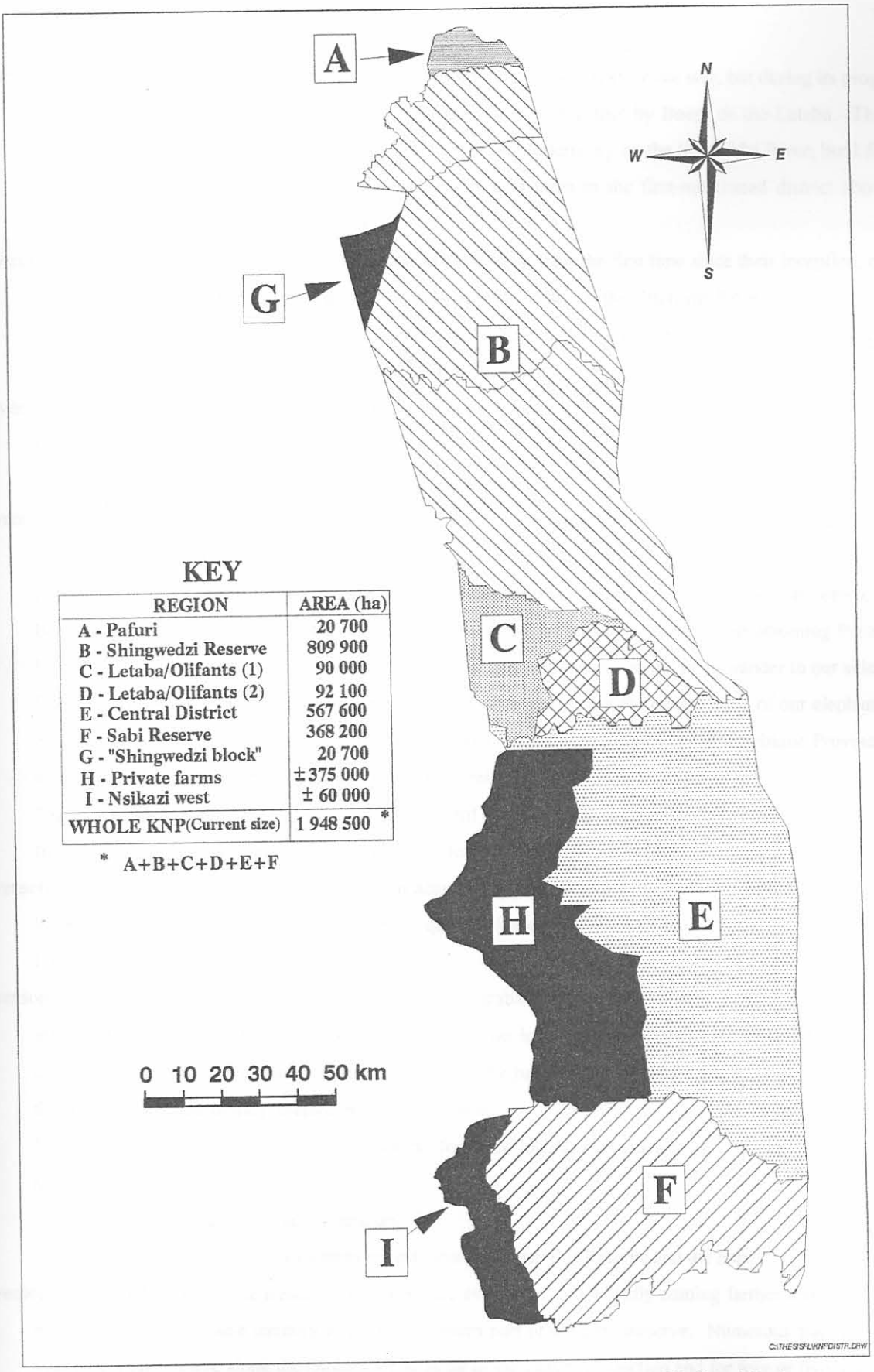


Figure 9: Historical area and boundary changes in the Kruger National Park since its proclamation in 1903 (see Table 3).

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(Stevenson-Hamilton 1903b). "Elephants have not crossed into the Transvaal since the war, but during its progress a herd came in from Portuguese territory and eight of them were shot by Boers on the Letaba. This was about the whole herd. There are still a few left in Portuguese territory on the Singwidsi River, but I fear we have seen the last of them in the Transvaal. Boers shot three in the first-mentioned district about two months ago (i.e. in Portuguese territory)".

(Stevenson-Hamilton 1905). "Elephants have appeared in the Reserves for the first time since their inception, coming from Portuguese Territory: four near the Singwitsi River, and six on the Oliphants River. It is quite possible that, finding themselves undisturbed, these animals may be induced to remain". (These animals may well be the remnants of the herd referred to by Vaughn Kirby (1896) - see above).

(Stevenson-Hamilton 1906-1907). "Elephants have very tentatively begun to make their appearance in some of their old haunts, but are evidently as yet by no means sure of their welcome. Fortunately, there are still a considerable number in the thick bush over the Portuguese border".

(Stevenson-Hamilton 1909a). "The facts were as follows: In 1902 a small Reserve (about 1 400 square miles) was declared in the Barberton District (Sabie Reserve). The following year, Government decided to proclaim as a Reserve practically all the country bordering the Portuguese border up to Rhodesia (Singwitsi Reserve), which, being a country well stocked with game would serve as a good "feeder" country from adjoining Portuguese East Africa. The natives all having guns there, the tendency of the game would be to wander to our side. This forecast has, indeed, since been fully borne out by results, and we owe the recuperation of our elephants, our elands, and possibly, in the extreme north, of our rhinos, to the contiguity of the Mozambique Province. The area so included comprised about 12 thousand square miles.

"At present there is permanently in the Reserve a herd of some thirty elephants, which originally crossed over from Portuguese territory, but now seldom, if ever, leave the Reserve".

(Stevenson-Hamilton 1911). "I was not successful in actually seeing any elephants during my annual tour this year though I spent some time in the district they frequent in hopes of doing so. Tracks were, however, fresh and fairly numerous".

(Stevenson-Hamilton 1912). "Major Fraser reports that considerable numbers of elephants have of late been coming into the Reserve from Portuguese territory consequent on hunting by natives on that side of the border. A considerable number were present during August near the junction of the Letaba and Olifants Rivers, both in the two Reserves and in the protected area between them.

"I think, however, that the following, allowing for unavoidable inaccuracies, gives a fair estimate, of the numbers as they stand at present:-

Sabi Reserve: "Elephant (migratory): 25

Singwidsi Reserve: "Elephants are migratory between this Reserve and the Sabi".

(Stevenson-Hamilton 1913). "Sabie Reserve. Elephants are every year undoubtedly coming farther and in increasing numbers from Portuguese territory in the north-eastern part of the Sabi Reserve. Numerous tracks were this year found everywhere along the Olifants River as far as the Imbabate junction and for four or five miles south of the former river. The state of the bush within this area shows it to have become a permanent feeding

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ground. By day, however, the elephants usually retire to the Lebombo Hills, or seek the shelter of a large and dense bush not far from the boundary. They cross the Olifants freely and wander all over the protected area for a distance of at least twenty miles from the Portuguese border.

"Singwitzi Reserve. Elephants are much more numerous than in the Sabi. The herds crossing from Portuguese territory wander the whole length of the Lebombo between the Letaba and Limpopo Rivers and also travel up the former river for a distance of forty miles or more from the boundary, sometimes crossing into the protected area".

(Stevenson-Hamilton 1914). "Singwitzi Reserve. The Elephants have been seen as far in as 40 miles west of the Lebombo, and as they are not interfered with I have no doubt they will forsake Portuguese Territory and make their permanent home in the Game Reserve".

(Stevenson-Hamilton 1920). "Sabie Reserve. These are such very slowly breeding animals that no striking increase is apparent. Their tendency however seems to be to live less in Portuguese territory and more in the Transvaal than formerly. They now wander, during the wet season especially, long distances into the Game Reserve, especially along the Olifants River and to the south of it near the Border.

"Shingwedzi Reserve. The same herd that is found near the Olifants River frequents the southern part of the Shingwedzi Reserve and appears on the whole to spend the greater part of its time therein".

(Stevenson-Hamilton 1924). "Twenty years ago the elephant was extinct in the Transvaal; but a good many still remaining across the border in Portuguese territory small parties gradually filtered back, until now we possess several herds of quite respectable dimensions, and somewhat embarrassing confidence".

(Stevenson-Hamilton 1925). "There are now two main herds permanently located within the Reserve in the neighbourhood of the Letaba and Tendi River, and they extend their wanderings to the north as far as the Shingwedzi, and south as far as the Olifants Rivers. In addition, a good many of the species, scared by the shooting which has been taking place on Portuguese Territory, have been migrating thence into the Reserve between the Shingwedzi and Limpopo Rivers, and were there encountered by the Government survey party, during the latter part of the year".

(Stevenson-Hamilton 1930). "Elephants have caused so much damage to native crops on the Letaba that the people of Knaba have had to be moved to a point some distance south of that river. These animals have also done some damage to the Olifants pontoon by breaking the wire cable stays, and have attempted to interfere with the cable itself. The animals which wander south to the Olifants River are invariably bulls, either singly or two or three together. The breeding herd is very local and seldom moves from its portion on the Letaba west of the Tendi Junction".

(Rowland-Jones 1955). "I have, for many years, interested myself in the gradual rehabilitation of the elephant in the Park, and I have taken every opportunity of trying to ascertain the position as it was at the beginning of the century.

"In 1931 one elephant made its appearance on the Pongola River and the natives informed me that this was spoored back to Malonga and was in fact the first scout to enter the northern area from Portuguese Territory. The following year a few elephant could be found at Malonga and ten miles further south at Wambia pans, but

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no other infiltrations occurred in other parts of the Park.

"This leads me to believe that the present population is derived from two sources; south of the Shingwidzi River the increase and gradual spread of the breeding herd at Letaba and to the north a small influx of elephant from Portuguese Territory through Malonga and Wambia.

(Stevenson-Hamilton 1931). "Elephants in small parties of bulls only, come south of the Olifants River in the east part of the section during the late summer and early autumn months in search of marula fruit. In the western part of the section near the Mklasiri River (the boundary) portions of main herds are however more or less permanently found. There is no doubt that the tendency of all the elephants is to move gradually westwards, where the country is richer and probably they will continue to do this until they come up against occupied land.

"Elephants (small parties of bulls) frequent the lower Letaba finding resting places in the islands in the river and they also wander across to the Olifants. The breeding herds are found higher up about 20-30 miles above the ranger's station. The latter has several times encountered considerable herds while on patrol, and when guiding the Schomburg filming expedition, he was able to bring them up to two sections of the herd - one of 60 and the other of 30 with a number of small calves. It seems certain however that the elephants generally still migrate periodically into Portuguese Territory at certain seasons of the year where no doubt a few get killed from time to time, although fortunately there is no considerable native population in that area of the Portuguese border.

"Elephants have recently come into the section (Punda), though at present they do not appear to remain in it permanently".

(Stevenson-Hamilton 1932). "It is now definitely established that there are three main breeding herds in the northern portion of the Park, aggregating probably not less than 150 animals in addition to which there are various small parties of unattached males moving about. The breeding herds keep as a rule to the west of the Tende River and like to wander far up the Letaba, this having no doubt in former days been their favourite area. A herd has in fact been known to go as far as the Mklasiri River which is far to the west of the Park. I think the tendency of the herds is to migrate less and less into Portuguese Territory annually, as they find themselves undisturbed in the Park. Detached bulls have been seen on several occasions between the Letaba and Olifants Rivers, and small parties of them have been noticed by visitors drinking etc. at the Letaba opposite to the Camp".

(Stevenson-Hamilton 1933). "It is now known that there are five separate breeding herds, Ranger Crous having discovered the existence of two others along the Olifants River. The total number of animals in the Park cannot be less than 200. The herds from the Olifants wander west and south, and have been seen a long way outside the Park and well up the Klasiri River. The herds on the Letaba largely confine themselves to the immense reed beds found in that river, and the tendency is less to leave the Park for incursions into P.E.A. than it was formerly. During the marula - March and early April - all elephants are less static and wander far from their usual feeding grounds. Individuals and small groups, have been seen as far north as the Shingwedsi and also in the extreme east of No. 8 section".

(Stevenson-Hamilton 1934). "There is a gratifying and very noticeable increase among these animals, as well as a tendency to spread away from their favourite fastnesses among the reed beds of the Letaba River. Individuals

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have been located less than 20 miles from Punda Maria on the main road to the south, which may either have come thence, or from the Portuguese Territory to the east. The bulls in small groups or singly have always been prone to wander, but in September the ranger of No. 6 Section encountered a considerable herd of cows and young calves on the main road just south of the Letaba causeway. Elephants were seen on Klasiri Mond, the extreme western corner of the Park south of the Olifants River in July, and they wander a long way up the Klasiri especially in summer. The rangers of Nos. 6, 7 and 8 Sections have all reported elephants in their sections and a large number of calves".

(Stevenson-Hamilton 1935). "This species is certainly increasing in the Park both in numbers and in extent of range. It seems now definitely established in No. 8 section. Parties of bulls, and even cows with calves have been seen close to Letaba".

(Stevenson-Hamilton 1936). "These animals were seen in greater numbers by tourists in 1936 than in any previous season. They seem to be losing their shyness, and are found more often near the roads than formerly. They have spread all over the Sections of the Park north of the Olifants River and are encountered equally in Nos. 6, 7 and 8 Sections. The increase of the elephant, which is of course an animal free from enemies except man, is more rapid than is generally believed. The gestation period is 22 months, and in a strictly unfettered state where there is plenty of space to roam and abundance of natural food, it is believed that the cows calve every two years or so, and that a female in her lifetime will produce a dozen or so calves, there is however no doubt some natural check to over-population such as infant mortality. Elephant calves in captivity are well known to be very delicate. Elephants are addicted to mopani forest where such exists, and this largely explains their preference for the northern portions of the Park. They are seldom encountered far south of the Olifants River except where mopani belts extend.

"There are now approximately 250 elephants most of the time in the Park as against an estimated 25 in 1912 and 0 in 1902".

(Stevenson-Hamilton 1937). "These animals have now spread all over Nos. 6, 7 and 8 sections, and are found permanently along both banks of the Olifants River, stragglers having ventured south to within 7 miles of Satara, and for nearly 30 miles up the Imbabate River. As regards vegetation however it must be admitted that the damage they do is almost unbelievable, as much in what they almost wantonly destroy as in what they kill in order to eat. Since elephants have increased and spread over the northern portions of the Park, they have destroyed many of the fine palm trees - some nearly 100 feet high - which used to grow on the swampy flats near the Shingwedsi and Letaba Rivers. The object is to get at the bunches of nuts growing at the crowns. An elephant will push down a large tree merely to pluck a few shoots from near the top or to get at a small piece of ivy growing on it, the latter being a favourite delicacy. No doubt this is one of Nature's methods of curtailing the otherwise too dense tree growth in a forest country. But where a herd of elephants has passed some time the bush looks as though a cyclone had passed through it.

"Since unrestricted shooting of elephants has been going on in Portuguese East Africa (about 12 months now), no doubt a great many animals have crossed into the Park, and I should estimate that the number here now must be at least 400. It is easy to distinguish these new comers from the old residents, since the smallest whiff

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of human scent is enough to send them off at once in panic".

(Stevenson-Hamilton 1938). "Owing to the abundance of food and water away from the rivers due to the heavy April rains which fell in the Olifants and Letaba areas, the elephants did not, during the winter, congregate much near these rivers, but were scattered through the bush. They were therefore not so easily or so often seen by visitors as in 1937.

"They are however spreading rapidly over the whole Park north of the Olifants River and are fast increasing in numbers. On the eastern border of No. 8 section around the Mnyonga pools the ranger reports the whole country to be a mass of elephant spoor. The dense bush here on both sides of the frontier and the entire absence of any human habitation on the Portuguese side make it an ideal retreat for the animals.

"The main breeding herds are elsewhere largely confined to the area between the Olifants and Letaba Rivers from some miles west of the tourist road to the western boundary of the Park.

"The herds of females and young ones are very nervous and suspicious, and keep far from all highways and human habitations; the parties of bachelor bulls, young and old, on the other hand, wander far and wide, and display no fear of, nor hostility towards motor traffic".

(Stevenson-Hamilton 1939). "Elephants are increasing, and are now spread all over most of the 4 northern sections. They are nearly always to be seen along the Shingwedsi River and its tributaries, as well as along the Olifants and Letaba Rivers, and nearly up to Punda Maria. Tracks of a single bull were seen in early November on the road only a few miles north of Satara, and they travel up the Imbabate at least as far as Chalons (following the mopani belt). The breeding herds confine themselves mainly to the area between the Letaba and Olifants Rivers above the respective causeways.

"Owing to the destruction by the summer floods of many of the large shade trees under which they liked to stand during the heat of the day, the small groups of bull elephants were less in evidence near the Olifants causeway than in recent years".

(Stevenson-Hamilton 1940). "The year has seen a wide expansion and a considerable increase of these animals. They are now encountered all over the four northern sections and have penetrated south as far as Isweni where at the end of the winter two bulls appeared near the W.N.L.A. compound where they tore down a notice board.

"Unfortunately a distinct migrating tendency westwards, at present confined to solitary bulls, is becoming apparent.

"Much damage is of course done to mopani and palm forest but in the former case this is certainly beneficial in keeping in check that extreme density of forest which inhibits the free growth of grass, while in the latter case it is beyond dispute that the elephants by their distribution far and wide of the undigested seeds of the palm fruit are the most potent factors in encouraging the spread of the various species which produce fruit eaten by them. Also having passed through one piece of forest and left a track like a tornado behind a herd seldom visits the same spot until a considerable time has passed, and it is remarkable to see how quickly an area apparently completely devastated regains its natural appearance.

"The experience from other parts of Africa shows that it is the large herds of females and young ones which do

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the real damage, once they have penetrated into cultivated area. This, in Uganda and elsewhere, has necessitated a system of 'elephant control' outside certain specified tracts of country. At first the scheme of allowing members of the public to shoot the elephant was tried, the administration taking half the ivory. This led, however, to all sorts of difficulties, and of course large numbers of elephants escaped wounded. Eventually only experts paid by government were employed and the whole of the profit on each elephant went to government funds.

"It is, however, likely to be a good many years before such a problem will have to be tackled in the Transvaal low-veld, and in the meantime I think shooting at raiding elephants by amateurs should be discouraged and the use of such other means as may suggest themselves, such as rockets, Veri lights etc., suggested against the solitary or pairs of bulls which so far are all that have to be contended against".

(Stevenson-Hamilton 1941). "The year was characterised by a great increase and local expansion of the elephant population of the Park. This no doubt is partly attributable to numerical increase by normal breeding, but also in considerable measure to the extensive hunting of elephants by natives which has, for some time past been legalised in portions of Portuguese territory adjoining the Park, and has resulted in a steady immigration from that country into the latter.

"During the year there became evident a tendency among the elephant population to move southwards as well as westwards. Up to 1940 lone bulls had seldom been reported even as far south as Satara, and then only during the marula season. Early in 1941 however, they began, singly or in small groups, to be seen in the vicinity of Tshokwane, and by mid winter had become more or less settled along the Manzemntondo River, with excursions as far south as the Mutlumubi River, 7 miles north from Skukuza.

"In September, possibly for the first time within nearly 100 years, elephants crossed the Sabi River to the south, and for some time about six of them were present near the Matamiri Spruit where it joins the Sabi about 19 miles from Skukuza. Here they were seen on several occasions by tourists. With the advent of rain towards the end of the year these animals seem to have returned northwards. Perhaps the prolonged drought which prevailed throughout the whole of the Olifants and Letaba areas for the first 11 months of the year, tended to decrease the food supply, and forced these small parties of bulls to seek a living farther afield. The dense wait-a-bit thorn bush characteristic of so much of the country along the south bank of the Sabi is probably less attractive to them than the more open veld with its numerous marula trees, palms and mopani forest in the north.

"Nevertheless, especially should the present and immediately following years be deficient in rainfall through the northern sections of the Park, there may be expected a further southern infiltration of small parties of (mainly) bull elephants especially during the autumn and winter months.

"On the other hand, should there occur heavy rainfalls, with consequently, plenty of food available, one may anticipate less tendency on the part of the animals to migrate from what are obviously their favourite habitats along the various rivers from the Olifants northwards. Further, if through lack of ammunition or other causes, the present killing of elephants by natives in P.E.A. should cease or diminish, there is a likelihood of a cessation of further emigration, and even a considerable return on the part of some of the herds to that country,

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which is throughout a large portion, very suitable to their habits".

(Stevenson-Hamilton 1942). "There was no further movement of elephants southwards from the Sabi River during the year. Ranger McDonald reported that those which were noticed in the vicinity of Gomondwane towards the end of 1941 had recrossed the Sabi to the north. Subsequent to the November rains in 1942 all the elephants apparently left the Sabi and returned northwards. A tour round the boundaries of No. 3 section from Crocodile Bridge via Lower Sabi to Skukuza by the Warden at the end of December revealed no recent traces of elephants, and such spoor as was noticed was at least two months old. Ranger Steyn also observed the tendency to trek north. It seems clear that the considerable southward movement from the Olifants and Letaba areas noticed in 1940-41 was primarily due to the drought conditions and consequent shortage of food in the favourite feeding grounds. Nevertheless, the trail having been "blazed" there is no doubt that elephants will at certain times of the year and under certain conditions continue to find their way at least as far as the Sabi River, where food conditions are good along the banks and on the islands.

"A single young male, apparently evicted from his herd, took up permanent quarters on the Sabi River from 2-10 miles east of Skukuza, and remained in that area from May until about mid-November. This animal was seen by many visitors during the season.

"Elephants, probably coming from the Imbabate River near the western boundary of No. 5 Section, where they have been localised for many years, appeared in the vicinity of Kumane, 16 miles south of Satara, but seemingly did not move east of the main road.

"It is the habit of elephants, like other wild animals, to frequent the neighbourhood of the larger rivers during the dry season, but after the fall of the first rains to spread themselves over the country, relying for water on the numerous bush pools and spruits which are dry in winter. It has thus happened in the past that the period of elephant assembly near the Letaba and Shingwedsi Rivers coincided with that during which the local camps were occupied by tourists. The lights, the noise and the scent of human beings evidently combined to deter the animals from venturing into the camps, and in consequence no instances occurred of the fences being broken or damaged, or of any attempted intrusions at such times. The dry period intervening between the departure of the visitors in October, and the signal for the annual migration of the elephants from the rivers, was usually so limited that the animals had no time to grasp and take advantage of the new conditions, and therefore the damage done was always quite minor and sporadic.

"The deserted state of the camps, during the whole of the dry season of 1942, however, encouraged a different attitude among the elephants, who were quick to take advantage of the absence of any large number of human beings. Very early in the winter individual bulls began to walk through the fences both at Letaba and to a lesser degree at Shingwedsi, the chief attraction to them being the large mlala palm trees which formed such an ornament to both camps, from which they chiefly coveted the nuts found growing on the crowns.

"Since the depredations always took place at night, it was most difficult to cope with them. The number of elephants visiting Letaba camp gradually increased, and it suffered in consequence more than Shingwedzi. Ranger Crous tried every method, short of using a rifle, that he could think of; firing at them with a shotgun,

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using flares, etc., but with no more than temporary effect. Nor is it probable that where, as at Letaba a considerable number of animals were involved, all or nearly all of them solitary bulls working alone, the shooting of one or two would have had any lasting effect. Within 3 months the larger palms in the camp had been destroyed, as well as all the smaller trees of such other types as were of any interest to the elephants. The camp fence was almost entirely flattened, throughout. The larger forest trees growing in the enclosure were too big to be tackled successfully, and so were left alone; no damage whatever was done to the rest huts or other buildings, nor in fact to anything except such items as furnished a source of food.

"At Shingwedsi the damage was confined in great measure to the acts of one large solitary bull, which also showed itself dangerous by chasing natives in the camp even in daytime, and in establishing something like a reign of terror, as he never moved away from the immediate neighbourhood of the fence. Instructions were therefore given for the killing of this animal, and were duly carried out by Ranger Tomlinson, who sat up for and shot it in the tourist camp, close to the camp officer's quarters, one night late in August. Not much damage accrued afterwards to the camp, and the palms therein had escaped extensive harm.

"It had been decided by the Board to experiment with an electric fence such as is in use at Addo Bush at the Letaba camp; but seeing that everything there which is likely to suffer had already been destroyed, it was agreed that it should be put up at Shingwedsi.

"It is understood that the shooting of elephants which was undertaken under government auspices in Portuguese Africa adjoining the Park, some years ago, and resulted in a considerable influx of these animals to the latter, has ceased for the past 12 months or more, and in consequence it is unlikely that there will be much more emigration westwards from that territory, where, especially in the north, there are very large expanses of suitable elephant country.

(Stevenson-Hamilton 1943). "Only a few straggling bull elephants are reported to have made their way south of the Sabi River. Two of these seem to have wandered as far as the Crocodile, towards the end of winter, as their spoor was seen by a native ranger patrol of No. 2 Section. Ranger James at once proceeded thither, and followed the tracks, which however led north and in fact the animals seem to have made straight for and crossed the Sabi, as about that time two bulls were known by their spoor to have passed close by Skukuza station during the night and crossed the Sabi to the north. No elephant remained, as last year, on the Lower Sabi road near Skukuza, and only 3 or 4 were reported in the winter near Lower Sabi and Gomondwane bush. Some appear to remain permanently along the Manzemntondo River, which is favourable country; but generally speaking the tendency is to return northwards towards the favourite mopani country immediately after the first rains have fallen, and the southward emigration in search of food seems to take place only in winter when conditions along the Olifants and Letaba become difficult for the animals.

"There are large herds along the Olifants River between the Imbabate and Hlalulume".

(Stevenson-Hamilton 1944). "Largely, no doubt, owing to the prolonged drought, elephants have been spreading themselves far and wide in search of food. Small troops of cows and calves have even been seen so far south as the Sabi River. Only isolated or pairs of bulls have ventured to the region of the Crocodile River and have never remained there, possibly because conditions are less tempting to them than further north where river

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banks are more abundantly clad. The rangers of Nos. 7 and 8 sections have been instructed to keep a strict watch and to destroy or scare any animals which may be found trying to cross out of the Park southwards.

(Stevenson-Hamilton 1945). "Drought conditions have favoured spreading of small knots of elephants over most of the Park. A group of 5 bulls is often present along the Mbeamide River, and sometimes moves southwards to the Crocodile, though it has not so far remained long in that vicinity. There are always a few present at Lower Sabi and Gomondwane. The tracks of one or two have been noticed as far West as Doispan.

"Ranger Crous reported a herd of about 70 with young calves at the river opposite Letaba Rest Camp. They are now nearly always to be found along the Pafuri River North of Punda Maria".

(Sandenbergh 1946). "With the exception of the South Western two thirds of Pretorius Kop area elephant are now well established throughout the Park. There is a good concentration of approximately 40 on the Crocodile River between the Mbeyamide River and Malelane. Five have been seen off and on for the last seven months on the Sabi River opposite Doispan.

"A rough estimate places their numbers at between 400 and 500".

(Sandenbergh 1947). "Elephant have continued their southerly movement and I am now convinced that they are firmly established in the south of the Park. During the year one was seen on the Little Faai in the Pretorius Kop area and, I think, one could reasonably expect them to be seen in most sections of the Pretorius Kop area within the next three years.

"South of the Sabi River I estimate the strength of elephants during 1947 to have been between 80 and 100; throughout all other sections of the Park elephant have been seen off and on throughout the year and an estimate I made during August leads me to believe that their numbers have now increased to nearer 600 than 500. There is no doubt that quite a few elephant came in from Portuguese territory - where the shooting of elephants has been going on throughout the year. The increase has also been good and we can expect elephant to break out to the West in fair numbers within the next few years. It is, of course, very difficult to say how many head of elephant the Park can carry but the fact remains that if they continue to increase, the time will come when the Park will not be able to support all the elephant in it and they will start leaving the Park in search of food".

(Sandenbergh 1948). "It would appear that elephant are increasing at quite a normal rate and that they are now very firmly established right down to the Crocodile River. They remained scattered rather late this year and appeared to be herding only as from July - this is most probably due to the fact that in the early part of the year the water distribution in the Park was better than usual.

"From information received from Portuguese territory, a considerable number of elephant were killed during the winter in areas not far removed from the Park, and as these areas are rapidly being denuded of elephant the result will be that we cannot expect to receive any major additions from that territory".

(Sandenbergh 1949). "It is my opinion that the Park is not yet fully stocked with elephant, but there surely will come a time when it will be, and set as it is, within a developed area, elephant will endeavour to break out from time to time. I believe, therefore, that whenever elephants break out with any determination from the Park, the wisest policy would be to have the animals in question killed. It would appear that, if left alone, these marauders

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return to encourage others to go out with them".

(Sandenbergh 1950). "Elephants are well established and increasing. Towards the end of the year there was a noticeable falling off in condition. This was quite normal in view of the drought conditions. The breeding rate appears to be well maintained and quite normal.

"During the year, for the first time, it has been definitely established that cows and calves have established themselves in the area South of the Sabi.

"The Pretorius Kop area, proper, was not visited this year, otherwise these animals can be found anywhere in the Park.

"In August, at the request of the Provincial Administration Park officials assisted in clearing the Blyde River area. Seven bulls were destroyed and the remainder trekked out, apparently to the Olifants River basin. No cows were seen in this area.

"In September elephants began breaking out over the Crocodile River and causing damage to European farms. Park staff destroyed seven bulls (six of which had previously been wounded by persons unknown). The remainder were driven from this valley. During the course of these operations it was established that there had been 40 to 44 bull elephants in the Crocodile basin. No cows were discovered. From the time of this operation no further trouble has been experienced.

From 1952 onwards, KNP reports were written in Afrikaans. For the purposes of this thesis, I have translated them into English. Any further text blocks in italics in this chapter have been translated.

(Raad van Kuratore vir Nasionale Parke. 1952). *"Two bulls which had been causing damage to crops were shot in March on the Shangoni boundary. One of the bulls tusks weighed 87 and 76 pounds.*

"Another bull was shot in May on Malelane Section after all possible methods of discouragement had been tried.

"So called "pilot bulls" ("spioenbulle" in Afrikaans) continued their history of dispersal into the South. Three bulls were seen at the famous hippo pool in the Pretoriuskop area and two (possibly three) crossed the western (Numbi) boundary at Mtimba. They soon returned to the Park after their reconnaissance".

(Steyn, L.B. 1955). *"For the Board's information and with a view to developments inside and across the Park's boundaries, I think that it would be useful and informative to give a short history of the distribution of elephants as observed by the Ranger Staff. The section of the report concerning the area to the north of the Olifants River has been prepared by Senior Ranger Rowland-Jones* (see below) *while that to the south has been drawn up by me.*

"Elephants were seldom seen to the South of the Olifants River before 1938, but the start of the penetration from the north was observed that year, led by "pilot bulls", which took them to the southern and across the western boundary. There are signs that even south of the Sabie the distribution towards the west is continuing.

"Elephant breeding herds established themselves throughout the area between the Olifants and Crocodile rivers between 1938 and 1944 and they are apparently established throughout the Kruger National Park".

"When this dispersal began in 1938, the population of the KNP was estimated at 244, all north of the Olifants

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River. According to the most recent game counts of 1954 the total is now 560 north of the Olifants and 180 to the south thereof, a total of 740 which represents an increase of 500 in the whole park over a period of 17 years.

1938-40: "The first penetration southward from the area between the Olifants and Letaba rivers into the Satara Section occurred during this period. Without even establishing themselves here first the dispersal continued south into the Tshokwane Section and the two Sections were colonised simultaneously.

1940: "Two bulls were recorded for the first time on the Esweni River near the Lebombos in June.

1941: "Bulls spread south of the Esweni and have increased to six. This dispersal occurred from the north along the Lebombos to Saliji in June and later to cross the Sabie in September 1941. In November, the first cows with oldish calves were seen in the Manzentondo River. In the mean time, bulls spread all over the area between the Olifants and Sabie rivers.

1942: "By May there was large herd of about 25 elephants in the area to the north-east of Tshokwane and in June a cow with a small calf (which must have been born in the area) was seen in the Manzentondo north west of Tshokwane. By the end of the year, a breeding herd of 35 were counted in this area and became permanently established on the Tshokwane Section. A herd of 12 established themselves in the Sabie River during the year wherefrom they spread to the Ngomondwane in the Crocodile Bridge area.

1943: "While the herd of 12 moved westwards from the Crocodile Bridge area into the Malelane Section, a gradual increase occurred in the area to the south of the Olifants River. No records were kept of the routes or numbers after this but from 1944 onwards elephants were permanently established south of the Sabie River. The numbers stayed reasonably low in contrast to the Area between the Sabie and Olifants rivers. Thirteen elephants were destroyed along the Crocodile River however for control purposes between 1946 and 1954. There are now an estimated 25 according to the most recent counts.

1944-45: "During the past ten years the elephant population increased steadily in the central areas and their numbers are now estimated at 255 while in the north they are estimated at 560.

Once the whole Park had been colonised, movements began to occur over the eastern and western boundaries. Before 1946 there were already forays over the eastern boundary between the Olifants and Sabie rivers and control of these miscreants had been initiated and of course still continues (but now by the Provincial Administration).

1946: "Control of elephants which crossed the Crocodile River began in 1946 and has continued sporadically since. Dispersal over the western boundary between the Sabie and Crocodile rivers has not yet developed to any significant degree but the signs are that things are gradually developing in this direction".

(Rowland-Jones 1955). "During the summer months of 1946, 47 and 48 after the first good rains a yearly migration occurred from Malonga to Klopperfontein and the area north of that to the Levubu, and it was not until 1949-

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50 that elephant took up permanent residence there. Again the reason was drought, the Wambia pans and others along the eastern boundary were completely dry.

"In 1951 the elephant had crossed the Park to the western boundary and the first scouts appeared in the native locations to the west.

"Meanwhile the elephant population at Shingwidzi increased at the same rate, the portion north of the river being fed by elephant movement down the Pongola river to the Shingwidzi, as the upper pools dried off.

"As these elephant became more and more permanent residents, Pafuri became a favourite winter resort with its permanent river water supply, but the population there varies yearly according to the rainfall. In my opinion there has been only a very small influx from Rhodesia as elephant from there mainly come down to the Limpopo during the dry months and re-cross after the first good rains.

"In 1952 the breeding herd at Punda Maria moved down the Pongola river as far as the Shingwidzi and since that period its habitat has been the Pukwane-Pongola-Shingwidzi block. This is still the only herd of any size which moves as far west as the Shangoni section and on the remainder of that area only a few bulls and an occasional cow are to be found.

"Meanwhile in the Shangoni area the first penetration had commenced. A limited number of elephants have been shot by Fauna and Flora in these areas, but the crucial fact emerges that in no case had the original pathfinder elephant been shot, so the path was laid for others. Now that this elephant raiding of native lands has developed into a normal summer routine on the part of the elephants, it will require a major operation to stop this and it is improbable that even the most stringent measures will leave a 100% effect.

(Steyn 1958). *"A bull and a cow with a small calf were seen for the first time in the south-western corner of the Pretoriuskop Section, and when these animals establish permanent residence there, elephants will have dispersed and become established throughout the Park.*

"Larger and larger breeding herds are moving south from the Olifants River area and a trustworthy lorry driver counted a herd of 65 along the Lower Sabie road. This herd, which last year came only as far south as the Sabie River, now spends its time between the Sabie and Crocodile rivers.

"Respective estimates by the Rangers of the Park's elephant population are as follows:

> *"1938 - 244; 1954 - 740; 1957 - 1,355 ("With due respect for possible errors, a conservative total of 1 000 is considered appropriate).*

"The question of whether or not the time is rapidly approaching that the tremendous increase of this species should be internally controlled is receiving attention and a meeting of the Nature Conservation Department on the subject was held on 15 March". (No record of the decisions taken at this meeting could be traced).

(Pienaar 1958). *"The Letaba Section is still the heart of the elephant territory and centre of population recruitment. A total of between 450 and 500 is likely the maximum occurring in the area.*

"The Shingwedzi Section has two main herds totalling 140 -145 elephants. The Shangoni Section has approximately 75, and Punda Maria Section possibly no more than 80. The total for the north is set at 650 - 700.

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"The Central Region has little proper elephant habitat, resulting in a smaller elephant population of about 120 of which 75 occupy the Satara and Kingfisherspruit. Tshokwane Section carries barely more than 45.

"The total population south of the Sabie River totals around 75 of which there are 45 in the Crocodile Bridge, 10 in the Malelane, and 20 in the Pretoriuskop sections respectively. A large majority of these are bulls.

"A calf was born on the Crocodile River in October and another was reported from the Crocodile Bridge Section after the rains. It would thus appear that elephants have finally re-established themselves in this area where they were driven to extinction by man in the 1850's".

(Biologiese Afdeling, Jaarverslag 1959). *"At the beginning of May the elephants returned to Pafuri. These included three bulls and a herd of 25 which caused considerable damage in the fever tree forest, but moved off after the first summer rains. The aloes (A. marlothi) at Doispane and also along the Sabie River were almost completely eradicated by a herd of elephants".*

(Brynard en Pienaar 1960). *"During March this year during an aerial survey of Quelia breeding colonies, elephants were also counted. A total of 986 were counted of which 2 were recorded in the Southern, 261 in the Central and 723 in the Northern Regions respectively. The Southern Region was not covered adequately yet the impression gained was that during the summer months, only a small percentage of the elephant population is permanently in the area".*

(Biologiese Afdeling 1961). *"During the most recent winter season, a large scale southward movement of Tshokwane's elephant herds took place, and the animals stayed along the Sabie River until deep in October. Large numbers of breeding herds were seen during flights in a light aircraft over the northern regions during the anthrax campaign. The herds move over large areas in the north, splintering and then rejoining and as a result, no reasonable estimate of the population could be gained from the totals as it can be expected that several herds were repeatedly seen at different localities.*

(Natuurbewaringsafdeling Jaarverslag 1962). *"Although the proposed aerial census of elephants had unfortunately to be postponed again, aerial surveys to search for Queleas were conducted in especially the northern areas. In these areas a total of 597 elephants were counted. Due to the prevailing widespread distribution of water, conditions were not particularly favourable for a proper survey of this type.*

"Elephants entered the Pafuri area in larger numbers than ever from the middle of May until the end of June this year. At one stage there were no less than 33 counted at the Picnic Place and two smaller groups at Bobomene. Strangely enough the vegetation (especially Fever Trees) were not so severely damaged as in previous years. After the first good summer rains, the animals again left the area as usual".

(Natuurbewaringsjaarverslag 1964). *"The aerial census of elephants which has been eagerly anticipated for so many years was finally successfully conducted this year during the first week in August with the aid of a helicopter. The helicopter proved ideal for this purpose. The eventual census total of 2 374 is considered to be a minimum total which is thought very close to the actual total. It can be accepted as fact that the increase on the population of 624 over a period of slightly more than two years creates a completely false impression and does not represent the result of natural increase, but rather on a drastically improved census technique. Immigration from Portuguese East Africa either temporary or of a more permanent nature, could also have*

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contributed to the increased total. In March it was seen how two herds of elephants of 42 and 34 respectively entered the Park near the Kalabyene Spruit in the Lebombos. It is very possible that due to the tremendous drought large numbers of elephants (eg the 110 which were recorded at Pafuri during the census) came in search of haven in the Park from the sandveld regions of P.E.A.

"According to a life-table constructed from the aerial census data, it was calculated that the present number of elephants, if allowed to increase undisturbed at the present rate, could double in the next 20 years.

(Natuurbewaringsjaarverslag 1967). *"A total of 6 586 elephants were counted during the aerial census of 1967, of which 362 were recorded south of the Sabie River, 1 482 in the Central District, and 4692 in the Northern District. These totals represent an increase of 2 374 on the 1964 census total which can not be attributed to reproduction. It is believed that the increase is mainly attributable to immigration from Mozambique as a result of the unfavourable conditions there. The possibility existed that many of these immigrants would return to Mozambique after the rains. A second aerial census conducted at the end of the rainy season in March revealed however that the majority of the elephants that came into the Park were still here, and it would seem that they are here to stay. The March census total was 6 093 inside the Park with another 309 in the border strip in Mozambique. Further, it would appear that the old pristine elephant habitats between the Limpopo and Olifants rivers in Mozambique are currently fast becoming inaccessible to elephants, particularly the breeding herds. The possibility of large numbers of elephant emigrating to Mozambique during future high rainfall years seems remote, and the large residential herds in the Park are now beginning to create serious problems"*

The summaries from the respective annual reports subsequent to 1968 have not been included here as these include much irrelevant detail. Also, the subsequent annual aerial census reports contain most of the information on population trends which will receive more attention in Chapter 5 (The Elephant Management Era).

The increase in the population given in the above reports and up to 1967 are summarised in Table 4 along with the nature of the estimate and the source reference.

It is clear from this that the increase between the years 1960 and 1967 can not be due to biological increase alone. It is likely that the estimated totals prior to 1967 were under-estimates and that the first aerial census yielded a result much closer to the actual figure, suggesting the apparent massive increase over this period. It is unlikely that any of the estimates prior to 1967 have any real value compared with the latter ones using aerial census techniques. A second curve has been fitted to the graph by eye which is likely to resemble the actual population increase more closely. This would

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reflect biological increase and immigration from the neighbouring territories (Zimbabwe (Rhodesia) and Mozambique) as well.

Table 4: Estimates of numbers of elephants in the Kruger National Park from 1903-1967.

Year	Number	Nature of estimate	Source
1903	0	Estimate	Stevenson-Hamilton (1903a, 1903b)
1905	10	Estimate	Stevenson-Hamilton (1905)
1908	25	Estimate	Stevenson-Hamilton (1909b)
1925	100	Estimate	Stevenson-Hamilton (1925)
1931	135	Estimate	c.f. Pienaar, van Wyk & Fairall (1966)
1932	170	Estimate	Stevenson-Hamilton (1932)
1933	200	Estimate	Stevenson-Hamilton (1933)
1936	250	Estimate	Stevenson-Hamilton (1936)
1937	400	Estimate	Stevenson-Hamilton (1937)
1946	450	Estimate	Sandenberg (1946)
1947	560	Estimate	c.f. Pienaar, van Wyk & Fairall (1966)
1954	740	Estimate	Steyn (1958)
1957	1 000	Estimate	Steyn (1958)
1960	1 186	Aerial survey	c.f. Pienaar, van Wyk & Fairall (1966)
1962	1 750	Fixed-wing survey	Pienaar (1963)
1964	2 374	Helicopter count *	Pienaar, van Wyk & Fairall (1966)
1967	6 586	Helicopter count *	Pienaar (1967)

Another possible explanation for the sudden increase in the KNP population between 1964 and 1967 is that an exodus occurred then from these neighbouring countries into the KNP. However, we have no other evidence (e.g. an increase in poaching or the advent of civil war in these countries) to substantiate this postulation.

In 1967, annual aerial censusing of the population as well as population control (culling) were initiated. This signalled the start of the "Management era" during which the policy was to hold the population at a level of around 7 000. This era is covered in Chapter 5.

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RATE OF RECOLONISATION OF KRUGER NATIONAL PARK BY ELEPHANTS

The pattern of recolonisation of the KNP by elephants subsequent to 1903 (when there were no elephants) and up to 1958 (when they had finally been recorded throughout the area) is shown in Figure 10. These data and localities were derived from the reports of the earlier rangers and wardens given above. Dates and places were given in these reports, but it is impossible to infer the exact localities that such observations were made. For example, "Tshokwane" could mean anywhere on the ranger's Section named Tshokwane, or it could mean at the ranger's actual quarters. For the purposes of the present analysis the localities were assumed to be the actual places of the name given in the reports. Distances between these localities where elephants were first recorded were measured as straight-line distances on a 1:250 000 map. The recolonisation process is presented in three ways. The first is simply based on the time taken to spread from the point of origin (roughly midway between the Park's northern and southern boundaries) to the northern and southern extremities of the KNP. Northward to the Luvuvhu River (which was the northern border of KNP at the time) took until 1945 (40 years to cover the 292 km distance at a mean rate of 7.3 km/year) while the spread southward to the confluence of the Crocodile and Sigaas rivers, was slightly slower, taking until 1958 (53 years to cover 280 kms at an average rate of 5.4 km/year). The mean dispersal rate (286 kms over a period of 46.5 years) was 6.2 kms/year or 0.16 yrs/km.

In Figure 11, the times and distances between the successive points where elephants were recorded for the first time were plotted. Table 5 summarises these data. The correlation between the two variables was poor, and the assumptions pertaining to the data points are such that a "least squares" estimate of correlation is invalid. The poor relationship suggests that the rate of dispersal was not a function of time, but rather that some other factor(s), such as habitat quality, may be more important in influencing in the recolonisation process.

In a third approach I recorded the straight-line distances between the point of origin and each successive point where elephants were first recorded. This shows that the spread through the KNP did not occur at a constant rate (Figure 12). Both northward and southward trends were sigmoidal. Northward, this acceleration occurred about ten years earlier than southward. Two of the data points (Pretoriuskop and Shangoni) do not fit this pattern, but both of these were points located far to the west of their respective preceding points. Pretoriuskop is west of

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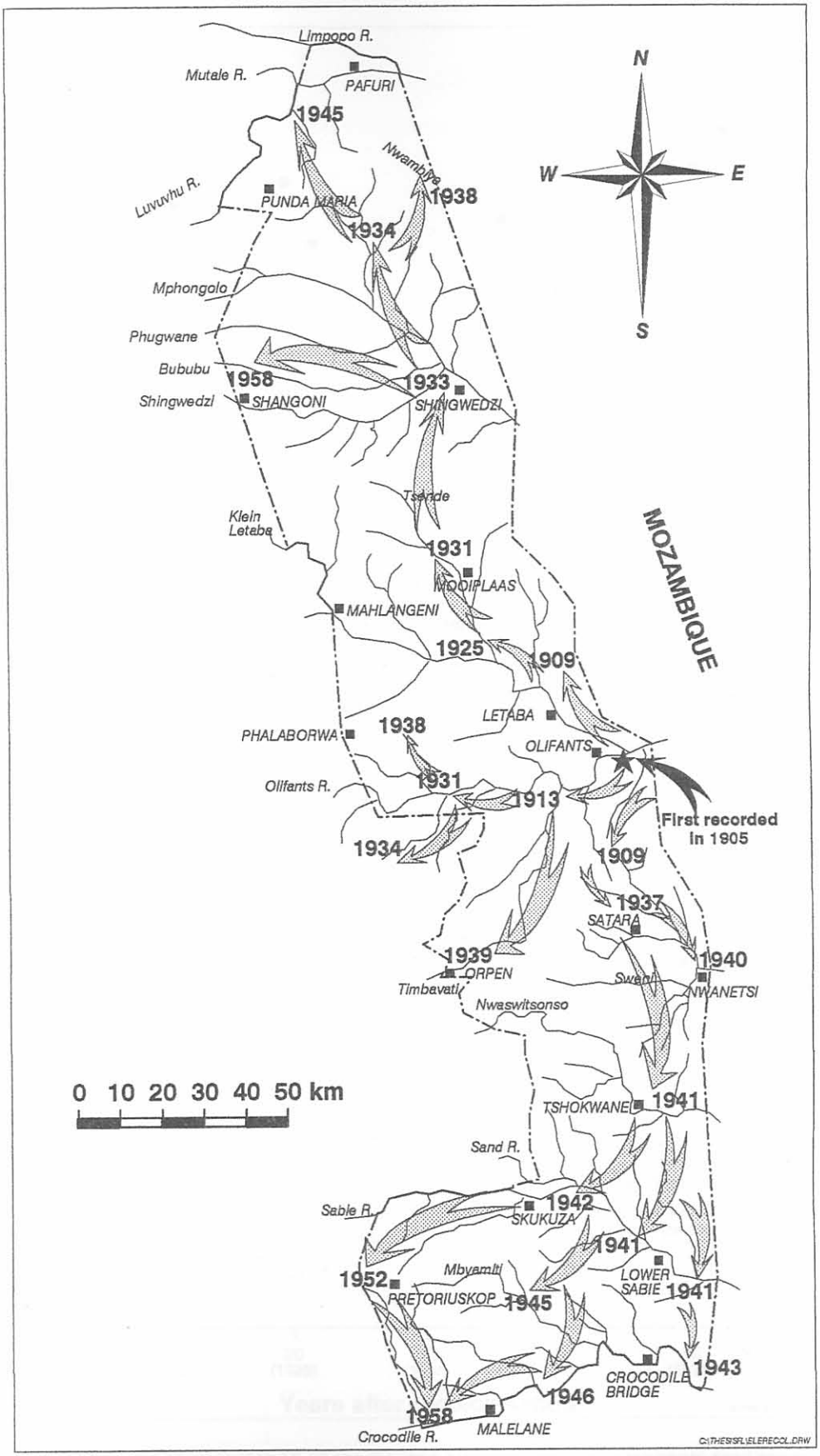


Figure 10: The recolonisation of the Kruger National Park by elephants subsequent to the arrival of the first Warden in 1903.

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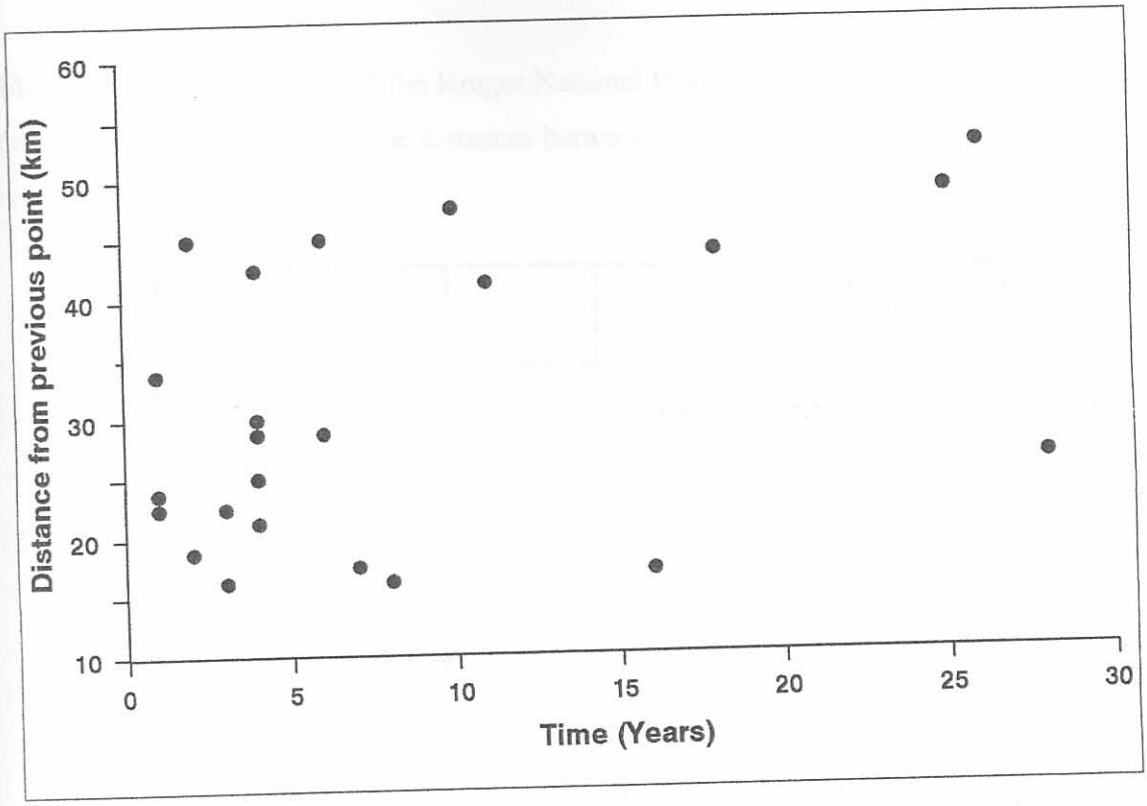


Figure 11: The relationship between time and the distance between successive points in the recolonisation of the Kruger National Park by elephants.

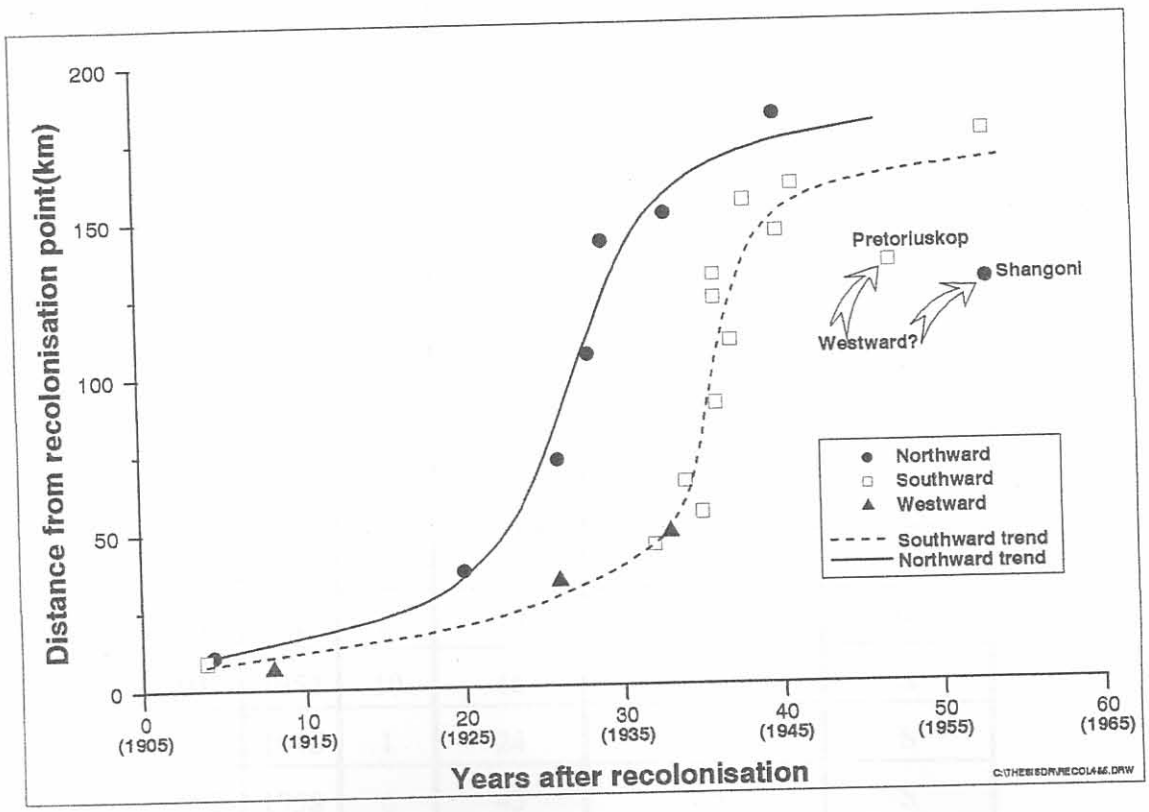


Figure 12: The rate of recolonisation of the Kruger National Park by elephants southward and northward between 1905 and 1908. The curves were fitted by eye and are based on data points illustrating the recolonisation process in Figure 10.

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Table 5: Recolonisation rate of the Kruger National Park by elephants between 1905 and 1958. Distances given are the straight-line distances between the successive points where elephants were first recorded.

Start date	End date	Time (Yrs)	Distance (km)	Dispersal rate (km/year)	Direction
1905	1913	8	16	2.0	W
1913	1931	18	44	2.4	W
1931	1934	3	16	5.4	S
1931	1938	7	18	2.5	N
1905	1909	4	25	6.3	N
1909	1925	16	17	1.1	N
1925	1931	6	29	4.8	N
1931	1933	2	45	22.5	N
1933	1958	25	49	1.99	W
1933	1934	1	34	33.8	N
1934	1938	4	29	7.2	N
1934	1945	11	41	3.8	N
1905	1909	4	21	5.3	S
1909	1937	28	26	0.9	S
1913	1939	26	53	2.0	S
1937	1940	3	23	7.5	S
1937	1941	4	43	10.6	S
1941	1942	1	23	22.5	S
1941	1943	2	19	9.4	S
1941	1945	4	30	7.5	W
1942	1952	10	48	4.8	S
1945	1946	1	24	23.8	S
1952	1958	6	45	7.5	S

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Skukuza along the Sabie River and Shangoni is west of Shingwedzi on the Shingwedzi River. This suggests that spread along a major river may have been slower than the spread between rivers. This is what could be expected as the less abundant water and food resources away from major rivers would probably have necessitated faster movement.

A second reason for these two points being inconsistent with the rest may be that although the respective distances between them and the point of origin were measured as straight line distances, the movement actually occurred in two phases - south or north initially and then west. The actual distance covered would thus have been further and, if measured this way, would conform more closely to the pattern.

ELEPHANT MOVEMENT BETWEEN THE KNP AND MOZAMBIQUE PRIOR TO THE FENCING OF THE BORDER

During the 1960's there was a fairly large seasonal movement between the KNP and Mozambique. It was realised that the fencing of elephants would be a problem, particularly on the eastern borders of the KNP. It was reported (Natuurbewaringsjaarverslag 1967) that *"The large-scale movement of elephants between Portuguese East Africa and the Lebombo flats of the Klipkoppies Section was again confirmed during the winter months this year. The movement is of such dimensions and is so regular that a conventional fence in this area would prove useless".*

This movement apparently resulted in a large influx of elephant from Mozambique sometime between the aerial censuses of 1964 and 1967 (see Natuurbewarings-jaarverslag 1967 above). Although it appeared that the majority of these animals had come to stay, there was still a limited movement across the border thereafter. In November 1970 an aerial survey was conducted in the area adjacent to the KNP in Mozambique in the triangle between the KNP in the west, the Limpopo River in the east and the Olifants River in the south (Joubert 1970). A total of 555 elephants was recorded and it was suggested (without substantiation) that a connection may exist between the elephant populations of the KNP, the Ghona-re-Zhou in Rhodesia (Zimbabwe) and the Save River in Mozambique. Another aerial survey was conducted in Mozambique in April 1972 in a strip 32 kms wide from the KNP's eastern boundary and between the Sabie River in the South and the Limpopo River in the north (Joubert 1972a). This time 789 elephants were recorded of which 120

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occurred to the south of the Olifants River and the rest (669) to the north. Based on the distribution of elephants and the apparent lack of permanent water in this area, in was concluded that 10 - 15% of the KNP's elephant population moved into Mozambique during the wet summer months and returned as the waterholes dried up. Although it was known that elephants moved across this boundary, the number of animals involved was not. Joubert suggested that this movement was not detectable from the annual census data (as would be suggested by large fluctuations in the census total from year to year) as these elephants would have moved back into the KNP each year during the time of the census.

In 1974 the South African Government decided to fence the eastern boundary in its entirety and this was completed by March 1976. This fence is substantial enough to limit the large-scale movement of elephants. Although still occasionally broken by adult bulls, it has stopped movements between Mozambique and the KNP such as those reported earlier (Joubert 1972a; Natuurbewarings-jaarverslag 1967).

Agostini (1994) contended that during the fencing of the KNP's eastern boundary in 1976, helicopters were used to drive "Mozambique's" elephants into the KNP before the fence was closed. The pilots employed by the National Parks Board at the time (H. van Niekerk & P. Otto pers. comm.[2]) and also those involved with fence construction deny this categorically, as does Pienaar (In litt.) who was the Park Warden of KNP at the time. Analyses of KNP aerial census data from 1967 to 1996 (see Chapter 5) also do not support this contention as it shows that the mean annual rate of increase of the elephant population declined from 9.8% to 6.6% after the fencing of the eastern and northern borders was completed. This suggests that until the fence disrupted it, immigration into the KNP was still taking place, and that there is no evidence of a "drive" of large numbers of elephants into the KNP at that time.

The fence between KNP and the private nature reserves on the western boundary between the Sabie and Olifants rivers was removed in 1994 to allow free movement of game. As the fence along the Limpopo River denied animals access to water in the dry season, it required constant maintenance due to the many breakages it sustained, particularly from animals like elephants and

[2] H van Niekerk and P. Otto, South African National Parks, Skukuza, South Africa.

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hippopotamuses. Maintenance of the fence was therefore suspended in the late 1980's and the remaining fencing material was finally removed in 1999.

THE HISTORICAL DEVELOPMENT OF THE CULLING POLICY

The artificial control of elephant numbers in the KNP had been discussed among staff as far back as at least the early 1940's. This is illustrated by an amusing excerpt which has been translated here from the diaries of one of the rangers of the time (Steyn 1942). *"With regard to the question of the control (culling) of elephants in certain areas where it may become necessary, the following idea came to mind, i.e. to use a 10 or 12 ton armoured car to remove them from any region. This will naturally only be possible after the present war and I leave the details to the imagination of the reader".*

During the 1950's and early 1960's there was a growing feeling among some biologists in Africa that elephant numbers should be controlled to prevent habitat change. Beuchner *et al.* (1963) concluded that in Murchison Falls National Park (Uganda) 4.5 - 5.5 elephants/mile5 was exceeding the carrying capacity and that "their numbers must be regulated to avoid damage to the vegetation and for the future welfare of the population of elephants". Similarly Glover (1963) felt that for Tsavo National Park (Kenya) "one elephant/mile^2 is apparently the highest stocking rate possible..." and that "If the habitat is to be preserved in its present form for all of the animals in the Park, then the numbers of elephants will have to be controlled".

These feelings were shared by the KNP's biologists who also felt that it may become necessary to limit elephant population growth in the KNP. This feeling was expressed by Pienaar (1960). "*The desirability of elephant control measures on a more general basis, which may become necessary in the near future, is a much more sensitive problem and will only be successfully solved after attention has been paid and information has been acquired regarding the actual numbers of elephant in the South, the number of breeding herds, herd composition, seasonal movements, ... as well as aspects such as how and where control should be applied*". In conclusion Pienaar (1960) made (among others) the following recommendations regarding the management of the elephant population:-

1. *That the collection of the information mentioned above be regarded as a matter of urgency.*

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An aerial census was suggested as the best means of obtaining the information.

2. *That in the light of the above information, an elephant population level be prescribed for the Southern District.*
3. *That all surplus elephants be destroyed annually through culling operations - preferably in the boundary areas and with due respect for outstanding individuals.*
4. *That during normal years, elephants be denied the strip along the Crocodile River as well as a belt along the western boundary.*
5. *Quantitative culling be applied elsewhere with great caution, if necessary".*

On 30 November 1965 a symposium was convened in Pretoria by the National Parks Board of Trustees (hereafter referred to as "the Board") which many South African biologists of the time attended. The symposium focused on "over-protection". Papers delivered at this symposium were on General Principles (Knobel 1965), Ecological Regions of the KNP (Brynard 1965), Problem Areas (van Wyk 1965), Reproduction and Biological Control (Fairall 1965), Control by diseases and Parasites (van Niekerk 1965), Animals, Areas & populations, Desirability of Culling and Methods (Pienaar 1965), Byproducts (Labuschagne 1965) and Publicity (van der Merwe 1965). The recommendation of this conference to the Board was that the numbers of seven species be artificially controlled by means of culling. The species involved were elephant, buffalo, hippo, giraffe, wildebeest, zebra and impala (Raad van Kuratore vir Nasionale Parke 1967). At its next meeting the Board decided that the culling of these species should take place (National Parks Board of Curators 1966).

Reporting on the census results of 1964, Pienaar *et al.* (1966) concluded that "It would appear that theoretically a carrying capacity of 1 - 4 elephants per square mile, depending on the existing vegetation, available water supplies and size of the area, holds for the majority of elephant habitats in Africa", and van Wyk & Fairall (1969), from the results of their research on the impact of elephants on the vegetation of the KNP, concluded that "... the highest number of elephants which could be carried .... would be 0.75/mile^2 (i.e. 6 000 elephants) if the total destruction of the vulnerable areas near water is not to result".

Pienaar (1996) also stated that this coincided with results obtained during the first helicopter census

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in 1964, *"... 1 139 elephants occurred in the Letaba River and its main tributaries (namely the Ngwenyene, Tsende, Shipikane, Makhadzi and Mbyashishe). This was apparently the preferred habitat of these animals ..... in which they stayed during the recolonisation years until they approached a natural saturation point before they, in ever increasing numbers, began to disperse northward and later southward... Because the recolonisation of the Letaba-Tsende area, which can be considered as prime elephant habitat, could occur without hinderance or human interference, it must be accepted that the elephant density per unit area during the continuing process of dispersal would give a very good indication of a self-imposed (ie natural) saturation level for elephants in this habitat. A planimetric calculation of the area of this original elephant homeland yielded an area of 1 030 mile² - that is one elephant per mile²".*

From this and the findings reported by van Wyk & Fairall (1969), the Director of the National Parks Board (Mr Rocco Knobel) recommended to the Board at an ordinary meeting held on 17 June, 1968, that the recommendation contained in Annexure "B" of the agenda with respect to the culling of elephant and buffalo in the KNP be adopted. The Annexure read as follows: "Until the water provision program has been finalised in its entirety, both the elephant and buffalo populations of the KNP should be held at their current level...". At this time the latest estimate for the elephant population (1967 census) was 6 586. This recommendation was adopted by the Board. Although it is obscure when or for what reasons it was changed, this figure was later rounded to 7 000.

This then was the level (7 000) at which management attempted to hold the population. The policy was adhered to until 1995 when a moratorium was placed on culling heralding the post-management era, though the last culls took place in 1994. This era is covered in Chapter 6.

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CHAPTER 5: PART 1:
HISTORICAL REVIEW OF THE ELEPHANT MANAGEMENT ERA

INTRODUCTION

The management of the KNP elephant population can be considered to have begun once fencing of its boundaries was initiated in 1960. Once completed the fence effectively contained the population and only small numbers entered or left through breakages or where fences could not be permanently erected in riverbeds.

Population increases led to the initiation of a culling program in 1967, and although this management action continued until 1994, the elephant management policy itself was only documented in 1986 (Joubert 1986).

FENCING OF THE KRUGER NATIONAL PARK'S BOUNDARIES

Information presented here on the fencing of KNP and elephant management policies are derived from a literature survey which included books, scientific literature, unpublished reports, annual reports from KNP, and diaries of earlier Wardens and Rangers. Sections of text in italics here and elsewhere have been translated by me from Afrikaans.

The fencing of the KNP was always held as an ideal by earlier managers. This is shown by Brynard & Pienaar (1961) who reported that "...while the fencing of the southern and western boundaries progressed slowly, it was seen how a long-cherished ideal was materializing, it was realised more and more that this is one of the most progressive steps ever in the protection and control of our wildlife populations, the curtailment of poaching and the preservation of our rare animal species". Fencing of the southern, western and northern boundaries was completed in 1961. The northern boundary fence ran along the northern banks of the Luvuvhu River to its confluence with the Limpopo River (note that this was prior to the area between the Luvuvhu and Limpopo rivers being proclaimed as part of the KNP, which occurred in 1969).

During the 1960's there was a fairly large seasonal movement between the KNP and Mozambique and it was realised that fencing along this boundary would be a problem. It

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was reported (Natuurbewaringsafdeling 1967) that *"The large-scale movement of elephants between Portuguese East Africa and the Lebombo flats of the Klipkoppies Section was again confirmed during the winter months this year. The movement is of such dimensions and is so regular that a conventional fence in this area would prove useless".*

During 1973 the authorities in Mozambique erected a fence along the eastern boundary from the Sabie River northwards to Mabakane Beacon (.45 kms). The fence was later considered to be substandard by KNP authorities and it was reported that it would ultimately have to be replaced (Natuurbewaringsafdeling 1974).

In 1974 political instability in Mozambique led to the South African Government deciding to fence the eastern boundary in its entirety. The requirements were that the fence should be game-proof, including elephant. By March 1976 the eastern boundary fence was completed and work commenced on the new northern boundary fence on the southern bank of the Limpopo River. This fence thus included the area between the Luvuvhu and Limpopo rivers which had been proclaimed as part of the KNP in 1969. In 1977 the stretch between Spokonyolo Pan and the Mutale/Luvuvhu confluence was completed while the fence along the Limpopo River was completed in 1978. The entire KNP was then fenced.

The eastern boundary fence is substantial enough to limit the movement of elephants. Although still occasionally broken by adult bulls, it has stopped movements between Mozambique and the KNP (such as those reported by Joubert 1972a).

These fences remained intact until 1994 when the fence between KNP and the private nature reserves on the western boundary between the Sabie and Olifants rivers was removed to allow free movement of game. As the fence along the Limpopo River denied animals access to water in the dry season, it required constant maintenance due to the many breakages it sustained, particularly from animals like elephants and hippopotamuses. Maintenance of the fence was therefore suspended in the late 1980's and the remaining fencing material was finally removed in 2000.

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The effects that these fences may have had on trends in the KNP elephant population are discussed later under "Rates of increase" in Part 2.

THE POLICY FOR THE MANAGEMENT OF THE KRUGER NATIONAL PARK ELEPHANT POPULATION

Elephant management was initiated in 1967, and Smuts (1974) reviewed the compartments in which culls were allocated, but it was not until 1986 that the management policy was finally documented (Joubert 1986) and is therefore included in this Chapter. In the management plan (or "Masterplan" as it was known) many of the management policies (other than those pertaining to the elephant population) were also finally formalised. This Masterplan acknowledged "that policies represent the dynamic aspects of wildlife management and are subject to amendments with the accumulation of information and revised interpretations" and it is the duty of the KNP Standing Committee for Wildlife Management to "revise the Masterplan ... on an ongoing basis, i.e. that additions and amendments to policies be recorded where applicable on an annual basis and that such additions/amendments be incorporated in a comprehensively revised Masterplan at five-yearly intervals and be submitted to the Board". It is therefore clear that, given information that indicates that current policies are not appropriate, they can be changed at any time. The following are brief, quoted summaries of the relevant principles and policies embodied in the most recent (1993) update:

The National Parks Act: ecosystem preservation - the basic issue

"The concept of ecosystem preservation is well established in nature conservation practice ... and is the primary objective for the proclamation of National Parks as defined in the National Parks Act (1976, as amended).

"This being the highest priority ... and, in fact, the legal responsibility of the Board, ... the preservation of structural and species diversity ... is an inherent part of ecosystem preservation".

Policies applicable to high-density species

"In the case of species whose population cycles extend over ... two or more climatic cycles, and especially where this situation may lead to:

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CHAPTER 5: THE ELEPHANT MANAGEMENT ERA (1961 - 1994)

PRELUDE

Elephant management in KNP began when the fencing of its boundary was initiated. The population's increase subsequent to the completion of the fence led to management actions to limit further population growth. This was mainly in the form of culling, though some translocations were conducted. Culling was terminated when an animal rights group FALCON (Front for Animal Liberation and Conservation of Nature) challenged SANP's right to kill elephants.

This challenge lead to a public debate held on 4th May 1995, in which SANP undertook to review its elephant management policy. A moratorium was placed on the culling of elephants until such review had been completed. The last culls were conducted in 1994. This initiated the post-management era which is covered in Chapter 6. The review has now been concluded and the new policy (Whyte *et al.* 1997; Whyte *et al.* 1999) is presented as part of this thesis in Chapter 7.

This chapter covers the era between initiation of fencing in 1960 up to the time that the moratorium was implemented in 1995. It is comprised of four parts. Part 1 is a historical review of the era, including the fencing of KNP and the elephant management policy of the time. Aspects of the dynamics of the population from data collected at censuses and culls are examined in Part 2, while a study of movements of radio collared elephants and the effects of culls on movements of these animals (from a paper by Whyte 1993) form Part 3. Part 4 is an analysis of census data examining the consequences of culling for the dynamics of the population compiled from a paper by van Aarde *et al.* (1999).

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1. Artificially high densities due to spatial limitations of the KNP.
2. Material changes in either the structure and/or composition of the woody element of the vegetation.
3. Changes in the structure and/or composition of the animal communities which may result in the impoverishment of such communities by affecting their structural and species diversity.
4. The artificial manipulation of such populations is accepted as a realistic and responsible management option".

"The only two known species to fall within this category are elephant and buffalo ... In both cases it is accepted, however, that under more natural situations their populations would also reach peaks and troughs and that such changes in population densities form an integral part of the functional aspects of ecosystems. Under the present circumstances it has become virtually impossible to assess the full implications of their ecological role in ecosystems. In spite of this situation it is imperative that special attention be paid to:

1. "The accumulation and assessment of data which could be of relevance in evaluating medium and long term population cycles.
2. "The influence of the long term maintenance of relatively stable population levels on other components of the ecosystem, in particular the vegetation and consequently also the associated animal populations.
3. "The possibility of simulating natural fluctuations in the management of these populations".

"Until such time that the required information is available, the objective continues to be to maintain the elephant population at 7 000, but accepting fluctuations between 6 000 and 8 500".

This policy was maintained until 1995.

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CHAPTER 5: PART 2: POPULATION DYNAMICS

INTRODUCTION

This part of the thesis is based on data obtained from the respective censuses of the KNP elephant population and on data collected during elephant culls conducted in KNP. Elephant censuses and culls were initiated in 1967. Censuses have been conducted annually since, but due to financial constraints, the census of 1979 was cancelled. Population reduction campaigns were also conducted annually. These initially took the form of culling only, but once the methods and equipment were developed, live removals by chemical capture and translocation were also conducted.

Smuts (1975) conducted a comprehensive study of the dynamics of the KNP elephant population from data collected at culls. Data collection continued after Smuts' study until the suspension of culling in 1995. Analyses of these data have revealed little that differed from Smuts' results and do not warrant further attention here. Analyses presented here are rates of population increase, mean calving interval (MCI) (as these differ from Smuts' findings) and an estimate of mortality based on the difference between potential and actual rates of increase.

MATERIALS AND METHODS

Census methods

No detailed description of the census technique employed for elephant in the KNP has yet been published. Joubert (1983) gave a brief description and Whyte (1996a) gave a detailed account with respect to buffalo. As this technique is fundamentally different to those used for censusing elephants elsewhere in Africa (e.g. Douglas-Hamilton 1996; Jolly 1969; Mbugua 1996; Norton-Griffiths 1978), a full description of the KNP technique is given.

Censuses were always conducted during the last two weeks of August and the first two weeks of September to capitalise on the late dry season conditions. At this time of year the animals tend to congregate in the vicinity of watercourses and waterholes and visibility is at its best due to the trees having shed their leaves.

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The aircraft used during most of the study period of the study was a four-seater Bell 206 Jet Ranger helicopter but a Eurocopter EC120 was used in 2000. A helicopter has a considerable advantage over fixed-wing aircraft in that it has extremely good forward visibility and can hover as well. Flying low and slow over the backs of the animals in the herd causes them to break away from the aircraft to the left and right thus splitting the group. Smaller groups can be counted more easily than larger ones. Also there is tighter control over the counting of these groups, particularly in large, loose aggregations of elephants, as the pilot can manoeuvre the aircraft systematically from group to group until all have been counted. In contrast, fixed-wing aircraft are forced to maintain forward speed which necessitates circling of the groups which is confusing to observers. The hovering capability of the helicopter allows the exact number of animals in the group to be counted as the helicopter can stay low over each group allowing counting and recounting until consensus of the group size has been achieved among the observers.

Because of its manoeuvrability, the use of a helicopter also allows the flying of a pattern which follows the watercourses (Figure 13). The KNP is particularly suitable for this as its undulating savannah terrain is drained by a well-spaced network of watercourses which are clearly visible from the air due to the fact that they are lined with tall trees. The pilot will begin by flying along one bank of a major watercourse, keeping close enough to it to allow careful scanning of this denser vegetation, but yet far enough from it to allow adequate scanning of the ground as far as the watershed. He then turns up each tributary and sub-tributary, following it up one bank to its source and back down the other bank. In this way each drainage system is systematically covered before moving on to the next. One of the advantages of this system is that it frees the pilot from the chore of instrument navigation. The watercourses give him visual cues as to where to fly and systematic ground coverage thereafter is automatic, which allows him to also function as an observer.

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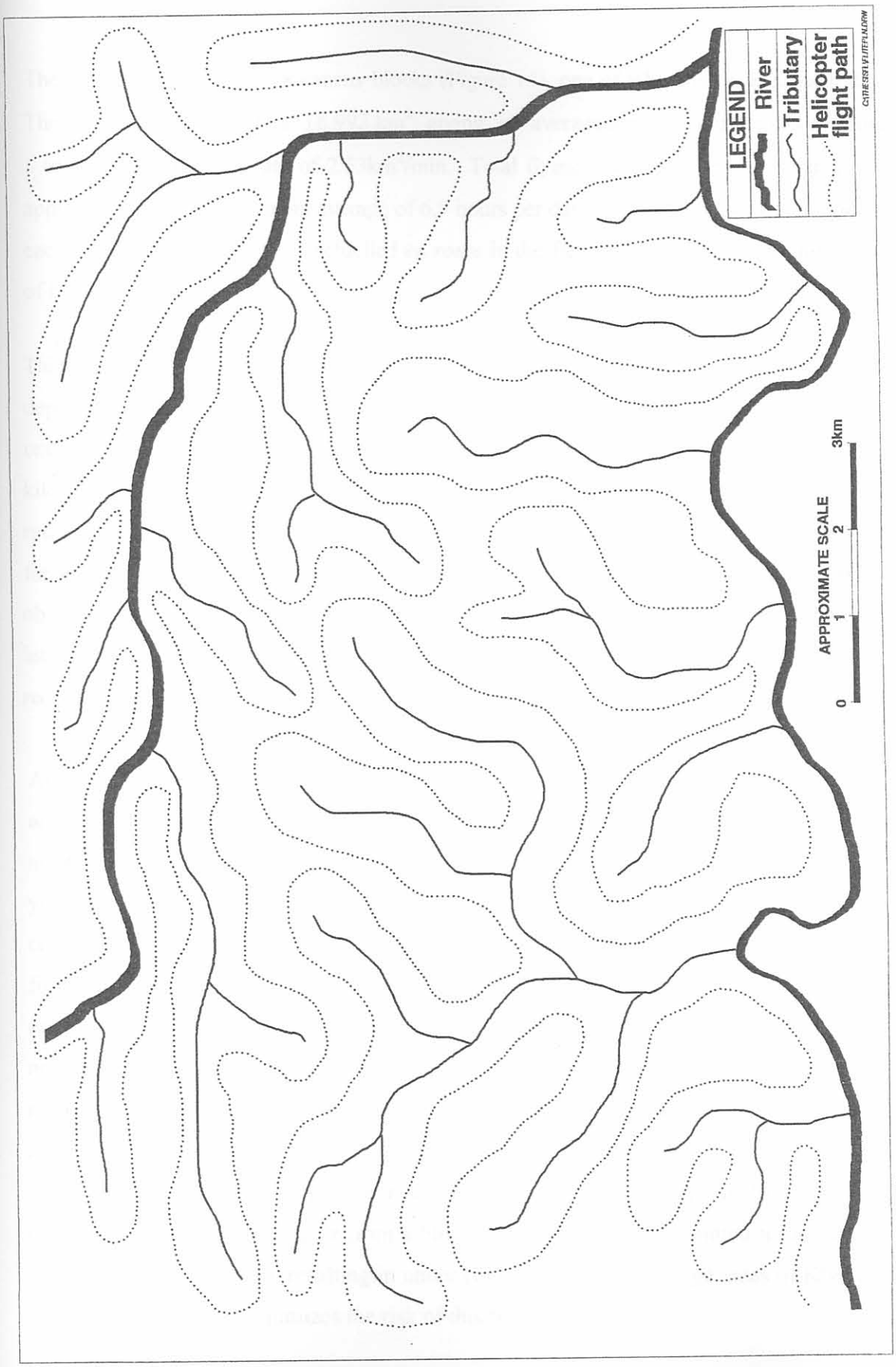


Figure 13: A graphic representation of the helicopter's flight path during aerial censuses of the elephant and buffalo populations of the Kruger National Park.

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The KNP is divided into 18 census blocks (Figure 14), one of which is covered each day. The total area of the KNP is 18 992 km^2 giving an average area covered per day of about 1 055km^2 and a search rate of 2.53km^2/min. Total flying time for the census averages at approximately 125 hours at an average of 6.9 hours per day. Usually three sorties are flown each day and the helicopter is refuelled *en route* in the field from a vehicle carrying drums of fuel.

The census is conducted at an altitude of between 170m and 250m above ground level, depending on the terrain and visibility. This altitude gives good visual coverage for about one kilometre on each side of the aircraft and, as the flight lines are seldom more than two kilometres apart, an almost total coverage of the area is achieved. Flight crew (pilots) are rotated to comply with aeronautical regulations, each flying for four days and then resting for the next four. The other crew consist of a navigator/data recorder and two other observers. Census data are recorded directly onto 1: 100 000 maps and were later digitised into a computer directly from these maps. Thus the distribution of the population is also recorded.

As is the case with all aerial census techniques, some degree of error will result from animals not seen and therefore not counted. The magnitude of error is unknown and can not be estimated, but because censuses are conducted at precisely the same time each year, it is assumed that the error is relatively constant from year to year. There is concern however, for the most recent census result as conditions were totally different from those experienced in the others (Whyte 2001 In prep.). The extraordinarily high rainfall during the preceding season led to summer-like conditions in which visibility and the distribution of the elephants must have been considerably different and may have resulted in undercounting. The census technique is prone to another form of error - animals crossing at night from one census block to another. This can either be movement from a block which has been counted to one which still has to be counted resulting in double counting, or from a block which must still be counted to one which has already been counted, resulting in under counting. However, large areas of KNP are censused daily which minimizes the risk of this type of error.

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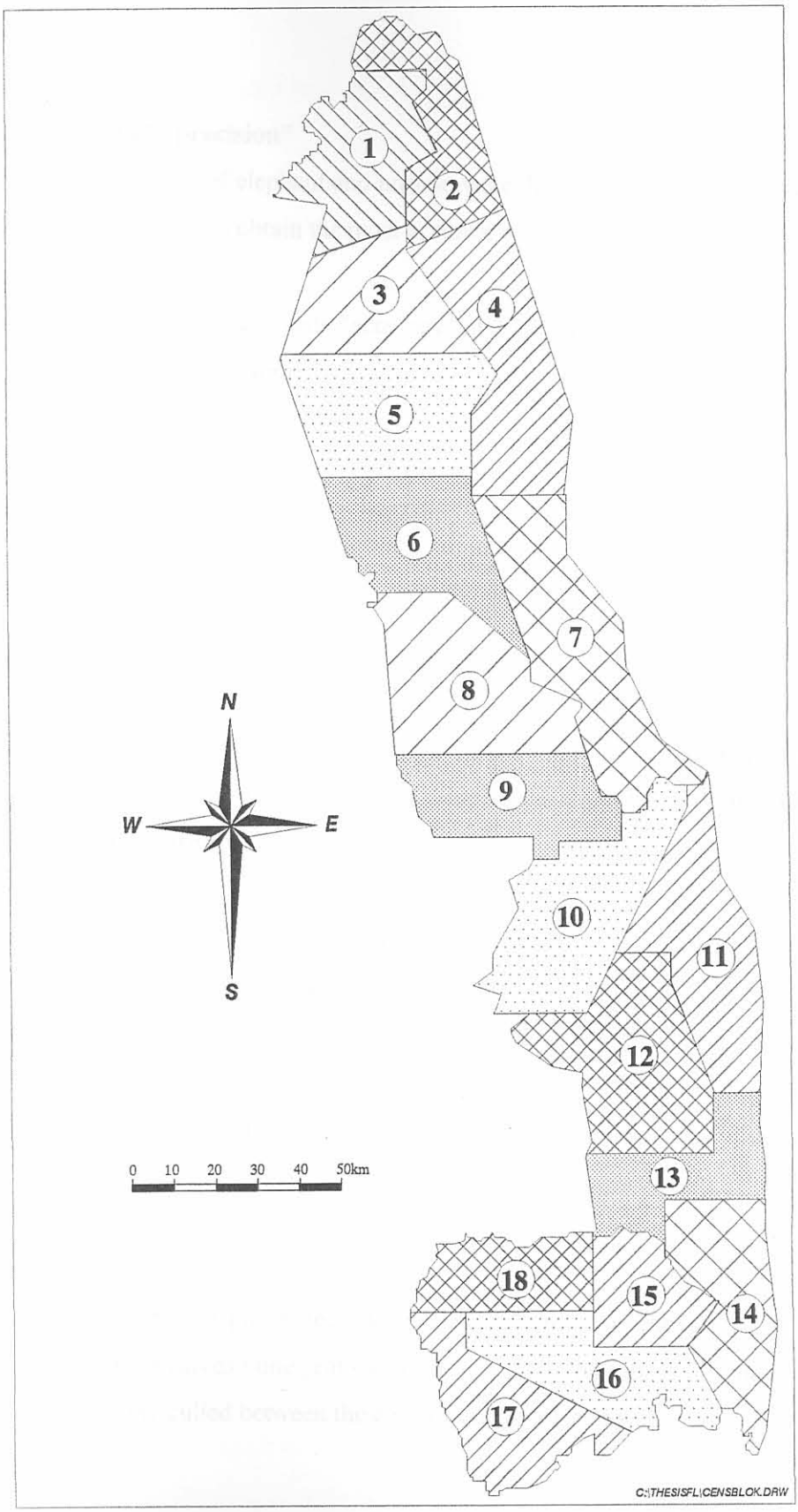


Figure 14: Aerial census compartments for the 18 days required to cover the total area of the Kruger National Park during annual censuses in August and September each year.

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Census "accuracy" and "precision"

Because annual culling quotas of elephant and buffalo were determined on the results of the censuses, SANP has attempted to obtain the most accurate and precise total possible.

In wildlife census terminology, the words "accuracy" and "precision" have fundamentally different meanings (Craig In litt.[1]; Norton-Griffiths 1978; Mbugua 1996). It can be assumed that different censuses of the same population of elephants will deliver different results even if the same technique is used. Should such different censuses yield results which are closely similar, the census technique is considered to be "precise", even though the result may not reflect the "true" population (the technique may deliver a consistent under-estimate). On the other hand, a technique which delivers a result which is close to the "true" population is considered to be "accurate", though the confidence limits may be wide (sample counts usually deliver such results). The accuracy of the technique used in KNP is not known. The census results have always been taken at face value by SANP and no further attempts have been made to statistically enhance the estimates or to determine confidence limits, such as could be obtained through repetitive sampling.

Since 1982 a simple calculation has been used in the KNP to give an estimate of the precision of each census. The previous year's census total was added to the current year's recruitment (the number of calves of under one year old recorded during the current census) and the number of elephants known to have been removed from the population since the previous census (mortality) was subtracted. This gives an "expected" census total. The equation reads:

$$N_{y+1} = N_y + B_y - C_y$$

where:

N_y = number of elephants recorded during the census of year y,

B_y = number calves <one year old recorded during the census of year y+1,

C_y = number culled between the censuses of year y and y+1.

[1] Dr. G.C. Craig, Department of Wildlife and Tourism, Botswana.

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The difference between this expected total and the recorded total gives some indication of the precision of each respective census.

There are three assumptions in this calculation. They are:

1. That the previous census total was "precise";
2. That natural mortality over the period between the two censuses was minimal;
3. That all calves of less than 1 year old are correctly classified as such.

The three assumptions were validated through the precision estimation method itself, the recording of fresh elephant carcasses during the census, and the experience of observers in the field age estimation of young elephants. Elephant carcasses never exceeded 0.04% of the total population and there was a high degree of observer consistency and experience in those who determined age classes of calves.

Culling methods

Between 1967 and 1994, the cull for any one year was conducted throughout the whole of the KNP, but since 1985, culling was conducted in one of the four management regions (see Figure 1) each year. These are the Far-northern Region (between the Limpopo and Shingwedzi rivers), North Region (between the Shingwedzi and Olifants rivers), Central Region (between the Olifants and Sabie rivers) and the Southern Region (between the Sabie and Crocodile rivers). The total cull of breeding herd animals for any one year was culled in one of these regions on a rotational basis. The elephant "sub-population" of each region was thus culled once in four years. The reasons for this were to try to reduce the stress which may be associated with such culling to once in four years, and to try to induce some measure of population fluctuation in each region.

The elephants to be culled were selected as randomly as possible. A target area was identified each day and the helicopter crew would search the area for the first suitable group in terms of size and locality. All members of the selected group were culled regardless of sex or age class. This was to ensure that the natural sex and age structure of the population was not artificially skewed as a result of selective selection of the elephants to be culled. Adult bulls occurred at a proportion of approximately 15% of the population in the first

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comprehensive aerial census in 1967. In order to maintain this proportion, the prescribed quota for bulls was always 15% of the total cull and 85% for breeding herds.

A herd of elephants is not a random mixture of animals but has a distinct structure, family members usually being in close proximity to one another, and each family is usually distinct from the next. The group selected for culling was thus usually comprised of one or more family units. These animals were then herded by helicopter to a suitable terrain nearby and all members of the group either culled or captured for translocation.

As a market existed for live elephants, not all animals were removed from the population by culling. Depending on the demand, a certain number were caught by drug immobilisation and translocated to other conservation areas each year. Until 1992 only juvenile animals were captured for translocation as the methods and equipment for translocating adult elephants had not been developed. The capture of juveniles continued until 1994, but since then, only whole family units have been translocated.

For reasons of the safety of personnel conducting the operation, the culling of elephants has always been conducted from a helicopter. For this same reason, the culling was conducted using the drug scoline (succinylcholine chloride) as this compound paralysed the animal, rendering it harmless once it was recumbent. In 1994 however, all elephants were culled by brain shot as it had been shown that the use of scoline was inhumane (Hattingh *et. al* 1984a; 1984b; 1990a; 1990b). In animals such as buffalo, the action of scoline is very rapid as all of the body's muscles are affected simultaneously and death is very rapid. In elephants the locomotory muscles are immobilised initially rendering the animal recumbent, and a while thereafter the diaphragm is affected, stopping respiration. The heart muscle continues to function and the animal eventually dies of asphyxiation.

Any of the culled animals still showing signs of life when the ground crew moved in, were immediately brain shot by a marksman on the ground. The throat of each dead animal was then cut to ensure proper bleeding as many of the products of the carcasses were used for human consumption. Carcasses were then loaded on to large trucks and transported to the abattoir at Skukuza.

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Methods used for elephant translocation

Prior to 1992, the means of moving adult elephants had not been developed, but markets existed for the restocking of conservation areas where elephants no longer occurred. Juveniles were captured by darting during culling operations. These animals were crated and transported to Skukuza where they were held prior to translocation to their destinations in batches. Once the equipment and methods to move even the largest elephants had been developed in 1994, only adult bulls or elephants in intact family units were captured for translocation.

All the elephants in a group were immobilised from a helicopter using the analgesic etorphine hydrochloride (M99: Kruger-Med Pharmaceuticals (Pty.) Ltd.), and the neuroleptic tranquiliser Azaperone (Stresnil: Janssen Pharmaceutica). The animals were revived using the antagonist (antidote) Diprenorphine (M5050: Kruger-Med Pharmaceuticals (Pty.) Ltd.) delivered intravenously (see Raath 1993 for further detail). Once they had all become recumbent, large elephants were rolled over their backs on to reinforced rubber mats using a hydraulic crane. They were then winched on these mats onto an articulating trailer which was then reversed up to a large "recovery" vehicle. This is a large trailer with doors at each end. This recovery trailer was positioned end-on to the transport vehicle. The immobilised elephants were winched into the recovery trailer where the antidote was administered. Once they had regained their feet the doors between the recovery trailer were opened and the elephants could be manoeuvred into compartments in the transport vehicle.

Once all the captured animals were loaded into the transport vehicle, they were dispatched immediately to their destinations as no veterinary quarantine regulations apply to elephants.

Logistics of the elephant management program

After the census of elephants in 1967 had revealed that there were at least 6 586 elephants in KNP, the culling program was instituted and was maintained on an annual basis until 1994. The management of the elephant population occurred on an annual schedule which began

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with the census in August/September. Once the census result was available, a culling quota appropriate to the maintenance of the population at a level close to that prescribed in the Masterplan (Joubert 1986), was proposed by the research officer responsible for elephant research. This was submitted to the KNP Standing Committee for Wildlife Management (and higher authority) for approval. The actual cull usually took place during the cooler months of the following year (April to August). Since 1985, the full cull for any one year was conducted in one of the four regions of the KNP on a rotational basis. This was implemented to try to induce a form of population fluctuation in each region, and to allow a three year period after a cull in which the animals would not be subjected to whatever stresses may be associated with such a cull.

Data collection at culls

Data pertaining to the dynamics of the elephant population were collected at culls from 14 different years, namely 1975, 1977, 1979, 1985, 1987, 1988, 1989, 1990, 1991, 1992, 1993, 1994, 1995 and 1996. The last culls from breeding herds took place in 1995, and in 1996, some problem bulls were culled. The database contains data from 4 739 culled and translocated animals. A sample of 2 790 breeding herd elephants and 503 bulls were examined at culls, and such data as could be collected from live animals were obtained from the remaining translocated elephants.

Whyte (1996b) reviewed the collection of data pertaining to population dynamics from dead elephants and the following were collected at culls: date, locality, and sex, age and reproductive status of every cow. This included checking for lactation, examining excised uteruses for pregnancy, and determination of sex and mass of foetuses. A device to assist with the determination of conception and birth dates from foetal age was developed (Whyte 1986; see Appendix 1). The proliferation of computers has rendered this device obsolete, but it is included in this thesis as Appendix 1 as it was used extensively for these calculations.

Age of each animal was determined from the molar dentition according to the method of Laws (1966). Although Jachmann (1988) refined Laws' technique, this was not used, as ages of earlier animals in the sample (1975 – 1988) could not be re-determined due to

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their mandibles having been discarded. A change in the age determination technique would compromise any comparisons between the two data sets.

Foetal ages were determined after the method of Huggett and Widdas (1951) which was refined by Craig (1984) for use on elephants. An average birth mass of 120kg after Perry (1953) was used and gestation time of 22 months (660 days) after Kenneth & Ritchie (1953) and Lang (1967). The equation used for determination of elephant foetal age in days was:

$$Age\ (in\ days) = (\sqrt[3]{m} / 0.945) + 183$$

(where **m** = foetal mass in grams – see also Appendix 1)

Rates of increase in the KNP elephant population

The observed rate of increase ($\bar{r}$)

The observed rate of increase ($\bar{r}$) is a general measure of population increase and is the exponential rate at which a population increases over a period of time. It was calculated as the slope of the straight line (of the form $y = a + bx$) connecting the points representing the Naperian logs of the two census totals (Caughley 1977). The slope of a straight line *(b)* connecting two points may be calculated by least square linear regression anlysis.

For KNP data this calculation was complicated by the annual removal of a proportion of the population by culling and/or translocation. The calculation could therefore not be made for a period longer than one year, but by adding the number of animals removed from the population between any two respective censuses to the N_{t+1} value, an estimate of $\bar{r}$ could be made for each year individually.

The censuses in the KNP were one year apart, so $Year_{t+1} - Year_t$ was always equal to 1. The denominator in the calculation could therefore be ignored, and as $\bar{r} = b$, the calculation of $\bar{r}$ became simply:

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$$\bar{r} = Log_e(N_{t+1}) - Log_e(N_t)$$

The mean of these annual estimates of $\bar{r}$ was then used to indicate the long-term rate of increase (the mean rate of increase had culling not taken place).

Potential rate of increase (r_p)

An estimate of "potential" rate of increase (symbolised here by r_p) was made from the proportion of adult (breeding) cows in the population and the MCI. From these two parameters, an estimate of the mean number of calves which should have been born annually to the population was calculated. This number, expressed as a percentage of the total population would indicate the potential rate of increase. The proportion of breeding cows in the population was estimated from this proportion in the culled sample. In each of the younger age classes (8 to 13 years) the number of cows either pregnant or lactating was counted. By 14 years, this proportion exceeded 90% so all cows older than 14 were considered to be breeders. This total was then expressed as a proportion of the total number of animals from breeding herds in the culled sample. From census data it is known that the population is comprised of 15% bachelor bulls and 85% in breeding herds, so the total number of breeding cows in the population could be estimated. Each of these should on average produce calves at the MCI, so the number of calves produced annually could be calculated. This number, when expressed as a percentage of the total population, represents an estimate of recruitment and is thus also an estimate of the "potential" rate of increase as it does not consider mortality.

The difference between the estimates of potential (r_p) and actual ($\bar{r}$) rates of increase then gives an estimate of the annual mortality rate (under the conditions prevailing in KNP), or

$$Mortality\ (m) = r_p - \bar{r}$$

Calving interval

The ratio of pregnant to non-pregnant cows in the culled sample was used to calculate the duration of anoestrus and the calving interval (after Hanks 1972) using the equation:

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$$\textit{Duration of anoestrus (x)} = \frac{\textit{Gestation time (Number not pregnant)}}{\textit{(Number pregnant)}}$$

where gestation time is 22 months (660 days) after Kenneth & Ritchie (1953) and Lang (1967).

Hence: $MCI = \textit{Duration of anoestrus} + \textit{gestation period}$

RESULTS

Census results

Since 1967, the KNP elephant population was censused annually using a helicopter. The aircraft type has changed from the initial use of a Bell G47 (until 1973), followed by Bell 206 Jet Rangers until 1999. These were replaced in 2000 by a Eurocopter EC 120. Observers and pilots have also changed, but due to the standardised technique (which has remained unchanged since 1967) and the long-serving nature of the staff involved, a high degree of continuity was maintained. It is believed that changes in crew and aircraft have not significantly affected census results

The respective census results show that the maximum population level achieved (prior to the implementation of the moratorium) was 8 678 in 1983 while the minimum total was 6 887 in 1985. This stability in the population was achieved through population reduction campaigns. Subsequent to the moratorium, the population increased from 7 806 in 1994 to 9 152 in 1999 but declined to 8 356 in 2000. Results of the respective aerial censuses subsequent to the implementation of the culling program in 1967 are given in Table 6.

Census accuracy and precision

Precision estimates are given in Table 7. The mean of these annual estimates of precision was 4.33 (S.D. 5.24). Up to the 2000 census, the difference between the recorded and expected results were very close, the largest being 7.9% in the census of 1986 with a mean difference from the expected of just 3.9%. The 2000 census result showed the biggest deviation from the expected (-12.1%). Including the 2000 result, the mean difference from the expected rose to 4.3%, but this still suggests that the census technique yields a high degree of precision.

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Table 6: Respective annual estimates of numbers of elephants in the Kruger National Park from 1967-2000 from aerial censuses.

Year	Number	Nature of estimate	Source
1967	6 586	Helicopter count *	Pienaar 1967
1968	7 701	Helicopter count *	Pienaar 1968
1969	8 312	Helicopter count *	Pienaar 1969
1970	8 821	Helicopter count *	Pienaar & van Wyk 1970
1971	7 916	Helicopter count *	Joubert & Pienaar 1971
1972	7 611	Helicopter count *	Joubert & Pienaar 1972
1973	7 965	Helicopter count *	Joubert & Pienaar 1973
1974	7 702	Helicopter count **	Joubert & Pienaar 1974
1975	7 408	Helicopter count **	Joubert & Pienaar 1975
1976	7 257	Helicopter count **	Joubert, *et al.* 1976
1977	7 715	Helicopter count **	Joubert & Pienaar 1977
1978	7 478	Helicopter count **	Joubert & Pienaar 1978
1979	No census	No census	No census
1980	7 454	Helicopter count **	Joubert 1980
1981	7 343	Helicopter count **	Joubert 1981
1982	8 051	Helicopter count **	Joubert 1982
1983	8 678	Helicopter count **	Joubert 1983
1984	8 273	Helicopter count **	Joubert 1984
1985	6 887	Helicopter count **	Joubert 1985
1986	7 617	Helicopter count **	Joubert *et al.* 1986
1987	6 898	Helicopter count **	Hall-Martin *et al.* 1987
1988	7 344	Helicopter count **	Whyte & Viljoen 1988
1989	7 468	Helicopter count **	Whyte & Viljoen 1989
1990	7 278	Helicopter count **	Whyte 1990
1991	7 470	Helicopter count **	Whyte & Wood 1992
1992	7 632	Helicopter count **	Whyte & Wood 1993
1993	7 834	Helicopter count **	Whyte & Wood 1994a
1994	7 806	Helicopter count **	Whyte & Wood 1994b
1995	8 064	Helicopter count **	Whyte & Wood 1995
1996	8 320	Helicopter count **	Whyte & Wood 1996
1997	8 371	Helicopter count **	Whyte 2001 (In prep.)
1998	8 869	Helicopter count **	Whyte 2001 (In prep.)
1999	9 152	Helicopter count **	Whyte 2001 (In prep.)
2000	8 356	Helicopter count #	Whyte 2001 (In prep.)

* Bell G47 helicopter. ** Bell 206 Jet Ranger helicopter. # Eurocopter EC 120

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Table 7: Estimates of precision in the respective censuses of the Kruger National Park's elephant population since 1982

Year	Recorded Total (B)	Calves	Cull	Expected total (A)	Difference B - A	% difference
1982	8051	-	473	-	-	-
1983	8678	763	1356	8341	337	3.9
1984	8273	305	1377	7627	646	7.8
1985	6887	296	369	7192	-305	-4.4
1986	7617	495	498	7013	604	7.9
1987	6898	157	304	7276	-378	-5.5
1988	7344	231	356	6825	519	7.1
1989	7468	220	366	7208	260	3.5
1990	7278	145	364	7247	31	0.4
1991	7470	141	358	7055	415	5.6
1992	7632	498	479	7610	22	0.3
1993	7834	278	390	7431	403	5.1
1994	7806	217	356	7661	145	1.9
1995	8064	815	127	8231	-167	-2.1
1996	8320	219	76	7927	393	4.7
1997	8371	433	51	8626	-255	-3.0
1998	8869	431	31	8726	143	1.6
1999	9152	220	12	9038	114	1.2
2000	8356	250	27	9365	-1009	-12.1

Culls and translocations

Between 1967 and 1999, 14 629 elephants were culled from the KNP population (Table 8). The minimum culled in any one year was 16 in 1981 and the maximum was 1 846 in 1970. The mean number culled was 502 per year. In 1966 and also between 1977 and 1994, juvenile elephants were captured during culling operations for translocation to other conservation areas.

This practise of translocating juveniles without their family groups was terminated in 1995 due to the perception that it was not humane. Since 1992, whole family units have been captured and translocated. Up to 1999, 72 adult bulls, 1 339 juveniles and 458 animals from family units have been translocated. In total, culling and translocation have collectively resulted in the removal of 16 498 elephants from KNP.

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Table 8: Annual elephant census totals and culling quotas in the Kruger National Park since the initiation of the census and culling programs in 1966 and numbers removed from the population.

Year	Census Total	Culling Quota	Total culled	Juveniles trans-located	Family units trans-located	Adult bulls trans-located	Total Removed after census
1966	No census	-	-	26	-	-	26
1967	6 586	650	355	-	-	-	355
1968	7 701	1 230	460	-	-	-	460
1969	8 312	1 408	1 160	-	-	-	1 160
1970	8 821	2 093	1 846	-	-	-	1 846
1971	7 916	889	602	-	-	-	602
1972	7 611	618	608	-	-	-	608
1973	7 965	738	732	-	-	-	732
1974	7 702	853	764	-	-	-	764
1975	7 408	601	567	-	-	-	567
1976	7 275	350	285	-	-	-	285
1977	7 715	663	544	26	-	-	570
1978	7 478	392	348	35	-	-	383
1979	-	380	322	48	-	-	370
1980	7 454	395	356	55	-	-	411
1981	7 343	71	16	0	-	-	16
1982	8 051	555	427	46	-	-	473
1983	8 678	2 229	1 290	66	-	-	1 356
1984	8 273	1 890	1 289	88	-	-	1 377
1985	6 887	369	268	101	-	-	369
1986	7 617	495	404	94	-	-	498
1987	6 898	305	245	59	-	-	304
1988	7 344	367	273	83	-	-	356
1989	7 468	367	281	85	-	-	366
1990	7 287	367	232	132	-	-	364
1991	7 470	367	218	140	-	-	358
1992	7 632	350	185	150	144	-	479
1993	7 834	577	308	74	8	-	390
1994	7 806	600	177	31	146	2	356
1995	8 064	0	44	0	83	0	127
1996	8 320	0	18	0	52	6	76
1997	8 371	0	5	0	12	34	51
1998	8 869	0	0	0	13	18	31
1999	9 152	0	0	0	0	12	12
2000	8 356	0	0	0	22	27	49
Total	-	20 169	14 629	1339	458	72	16 520

Rates of increase in the KNP elephant population

Observed rate of increase ($\bar{r}$)

The values of $\bar{r}$ for respective periods between censuses are given in Table 9. Due to a census being missed in 1979, estimates of $\bar{r}$ could not be made for the years 1978 and 1979,

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but the mean for the remaining 31 years was 0.075 (S.D. = 0.057). Between the two periods of the table (67 to 77 and 79 to 99) there was a clear difference in the mean values of $\bar{r}$. These were 0.098 (S.D. = 0.056) in the earlier period, and 0.058 (S.D. = 0.054) in the latter.

Figure 15 shows the individual values of $\bar{r}$ which indicate a declining trend, but over the full period a least squares regression gave a poor correlation ($r^2 = 0.297$). The trend appears to fall into three periods which may be related to fencing of the KNP's boundaries. The last of KNP's boundaries (the eastern boundary) was fenced in 1976 and between 1967 and 1976 (Period 1), the mean rate of increase was 0.104 (S.D. = 0.055). The western boundary fence was removed in 1994 and between 1975 and 1994 (Period 2) the mean rate of increase was 0.066 (S.D. = 0.047), while from 1994 to 2000 (Period 3), this rate declined to 0.015 (S.D. = 0.058). A one-way analysis of variance confirmed that there were significant differences ($F = 4.39$; $df = 2, 28$; $p = 0.02$) attributable to the respective periods, and multiple testing showed that the difference resided between Periods 1 and 3. No detectable trend could be found in the $\bar{r}$ values of the years in Period 2 ($r^2 = 0.0007$).

Potential rate of increase (rate of increase from MCI)

The age at which all cows were sexually mature was estimated from data from the culled sample in Table 10. At 14 years 93% of cows were either pregnant or lactating, so all elephant cows of 14 years or older were considered to be "breeding" cows (n = 1 174).

In the culled sample there were 119 breeding cows of 13 years or younger who were also either pregnant or lactating. This gave a total of 1 293 breeding cows from the total sample of 2 790 breeding herd animals culled. Breeding herds occur at a proportion of 85% of the KNP population (Whyte & Wood 1996). The breeding herd sample of 2 790 thus represents the breeding herd component of a population of 3 282. Of these, 1 293 were breeding cows (39.6%) each producing a calf every 4 years, or 0.25 calves per breeding cow per year. This sample of breeding cows would produce 323 calves in a year which represents a recruitment rate to the total population of 9.8%. This percentage also represents an estimate of the potential rate of increase in the absence of mortality.

Figure 15: Rates of increase ($\bar{r}$) of the Kruger National Park elephant population for respective years between 1967 and 1999.

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A similar procedure was followed for each year's calving interval from pooled results from Smuts (1975) and this study. The same assumptions were made – i.e. that the proportion of breeding cows in the population stayed the same. This allowed the calculation of the range of potential rates of increase in this study which yielded a minimum of 7.8% and maximum of 16.8% (S.D. = 2.72; n = 17 years).

Table 10: Reproductive status of elephant cows between the ages of 7 and 14 years.

Age	n	Not pregnant or lactating	Pregnant and/or lactating	% mature
7	74	74	0	0.0
8	75	73	2	2.7
9	75	66	9	12.0
10	74	42	32	43.2
11	32	16	16	50.0
12	32	7	25	78.1
13	44	9	35	79.5
14	90	6	84	93.3

Calving interval

Estimates of the calving interval from the proportion of pregnant to non-pregnant cows are given in Table 11.

The MCI over the 12-year period of the sample was 43.9 months (3 years and 8 months). This is shorter than that recorded by Smuts (1975) for the same population. In his total sample he recorded 292 pregnant and 430 non-pregnant cows. This gave an estimate of the MCI of 54.4 months (4 years and 6 months). The respective proportions of pregnant to non-pregnant cows in the two samples were significantly different ($\chi^2 = 15.1$; $p < 0.001$), but the means for the two samples were not ($t = 1.608$; $p = 0.129$). As the data were collected in an identical way, they were pooled (776 pregnant and 912 non-pregnant; n = 17 years) to give a MCI from both studies. This placed the MCI at 47.9 months (S.D. = 11.02) or 3.99 years which has been rounded to 4 years for further calculations made later.

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Table 11: Annual estimates of the calving interval in months from the number of pregnant and non-pregnant elephant cows recorded per culling year.

Year	No. pregnant	No. non-pregnant	Calving interval (years)	Calving Interval (months)
1976	12	6	2.8	33.0
1977	14	19	4.3	51.9
1978	29	25	3.4	41.0
1979	35	62	5.1	61.0
1987	55	73	4.3	51.2
1989	47	42	3.5	41.7
1990	39	64	4.8	58.1
1991	52	45	3.4	41.0
1992	39	55	4.4	53.0
1993	48	49	3.7	44.4
1994	82	23	2.4	28.2
1995	32	19	2.9	35.1
Totals:	484	482	3.7	43.9

Estimate of mortality rate

Although the mean observed rate of increase ($\bar{r}$) for the population over the full period was 0.075, the rate when the population was completely confined was 0.066. This must represent the best estimate of $\bar{r}$ as the population was not affected by immigration or emigration, and this was therefore the rate used in the calculation. The potential rate of increase (r_p) was estimated at 0.098 (see below) and the estimate of mortality was thus 0.098 – 0.066 = 0.032, or 3.2% of the population per year.

DISCUSSION AND CONCLUSIONS

Census results

Prior to the implementation of aerial (helicopter) censusing of the elephant population, estimates of the population were based on the opinions of individual Section Rangers. These had clearly been gross under-estimates as the first comprehensive aerial census

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revealed far more elephants than were expected (Pienaar 1967). The last estimate prior to this had been a population estimate of 2 374 in 1964 (Pienaar, van Wyk & Fairall 1966). The dramatic increase to 6 586 in 1967 gave impetus to the implementation of the culling program which was initiated in 1967 (Pienaar 1967).

The objective of the census and culling program was to maintain the population at a level of around 7 000. This is reflected in the respective census results as all population declines (except that shown in 2000) were induced through reduction campaigns. It is believed that the very low count in 2000 was the result of almost summer-like conditions which prevailed from the exceptionally high rainfall of the previous rainy season. These conditions were unlike any that had prevailed during all previous censuses. Trees had not lost their leaves which reduced visibility and surface water was abundant. The census technique of following drainage lines (where the only water is usually to be found at this time of year) was almost certainly compromised by a larger proportion of elephants occurring on the watersheds and thus being missed. Another possible factor negatively influencing this census result may have been emigration to the private nature reserves on KNP's western boundary. But given the uncertainties of censusing, the possibility exists that the difference was real. This will no doubt be revealed in future, more normal censuses.

Except for the year 2000, the population showed a sharp increase subsequent to the implementation of the moratorium in 1995. The increase can be ascribed to minimal population reduction campaigns over this period.

Census "accuracy" and "precision"

This equation used to estimate precision of respective censuses has been criticised (Butterworth, In litt.[2]) as it includes no estimate of natural mortality. He suggested a more appropriate equation:

$$N_{y+1} = N_y + B_y - D_y - C_y$$

[2] Prof. D.S. Butterworth, Dapartment of Applied Mathematics, University of Cape Town.

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Table 9: Annual estimates of the observed rate of increase ($\bar{r}$) of the Kruger National Park's elephant population.

Year	Census total A	Next census total B	Number removed C	Estimated population D (D=B+C)	$\bar{r}$ LogD-LogA
1967	6586	7701	355	8056	0.201
1968	7701	8312	460	8772	0.130
1969	8312	8821	1160	9981	0.183
1970	8821	7916	1846	9762	0.101
1971	7916	7611	602	8213	0.037
1972	7611	7965	608	8573	0.119
1973	7965	7702	732	8434	0.057
1974	7702	7408	764	8172	0.059
1975	7408	7275	567	7842	0.057
1976	7275	7715	285	8000	0.095
1977	7715	7478	570	8048	0.042
1978	7478	No census	383		
1979	No census	-	370	**Mean (1967-1977):**	**0.098**
1980	7454	7343	411	7754	0.039
1981	7343	8051	16	8067	0.094
1982	8051	8678	473	9151	0.128
1983	8678	8273	1356	9629	0.104
1984	8273	6887	1377	8264	-0.001
1985	6887	7617	369	7986	0.148
1986	7617	6898	498	7396	-0.029
1987	6898	7344	304	7648	0.103
1988	7344	7468	356	7824	0.063
1989	7468	7287	366	7653	0.024
1990	7287	7470	364	7834	0.072
1991	7470	7632	358	7990	0.067
1992	7632	7834	479	8313	0.085
1993	7834	7806	390	8196	0.045
1994	7806	8064	356	8420	0.076
1995	8064	8320	127	8447	0.046
1996	8320	8371	76	8447	0.015
1997	8371	8869	51	8920	0.064
1998	8869	9152	31	9183	0.035
1999	9152	8356	49	8405	-0.085
2000	8356	-	-	-	-
				Mean (1980-1998):	**0.058**
				Mean (1967-1998):	**0.075**

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where:

Ny = number of elephants present at the start of year y,
By = number born during the year y+1,
Dy = number dying of natural causes during the year y+1, and
Cy = number culled during the year y+1.

Theoretically the criticism is valid but the two equations are essentially similar. This is because By is different in the two equations. In his equation it represents the total number of calves born and thus it is essential to include an estimate of calf mortality. In SANP's equation however, By is the count of the number of calves under one year old which had survived until the next census. Young calves are the age class of the population which would experience the highest mortality rates, and as censuses are conducted exactly one year apart, mortality in this age class since the previous census is accounted for - calves that have already died are irrelevant. Also, very few elephant carcasses were recorded during censuses or reported by field staff, so natural elephant mortality rates are low in the KNP. Natural mortality will not likely be a cause of significant error in the estimation of the census result and census precision, and the exclusion of Dy is justified.

Due to the lack of estimates of the precision of the KNP census technique (such as could be obtained through repetitive sampling), the SANP equation has been used only as an indicator of the quality of the census. If the observed census result was within a few percent of the expected one, there was unlikely to have been a major flaw due to census error. The large difference obtained in the 2000 census result (-12.1%) is an indication that some error had occurred, which has been ascribed to the poor prevailing conditions and possible emigration from the population.

The low mean of the differences of the observed results from the expected suggests that the census technique yields a high degree of precision, but the accuracy of the technique remains obscure. While the high degree of precision indicates that a consistent proportion of the population is counted annually, the accuracy of the method (the proportion of the population not seen) still remains unknown.

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Rates of increase and calving intervals

Calef's (1988) model of the maximum rate of increase of an elephant population suggests that once the population had achieved a stable age distribution, it would grow at 7% per year given a MCI of three years. This concurred with the currently accepted maximum rate of increase which was reported for the Addo Elephant National Park (Hall-Martin 1980; 1984). However, a more recent study (Woodd 1999) suggested that this would not be sustained in Addo and predicted a rate of 5.2% if a stable age distribution was attained.

Differing rates of increase have been recorded in KNP for different periods of time. These ranged from 1.5% to 10.4%, but it seems certain that these were influenced by the erection and removal of fences, which initially affected immigration from Mozambique and later, emigration to the private reserves to the west. This is particularly true of the Sabi-Sand Private Nature Reserve, which in 1994 was known to have only 51 elephants (20 breeding herd animals and 31 bulls) prior to removal of the fence (Whyte & Wood 1994b). This area represented an almost vacant habitat for elephants. By the year 2000 this population had increased to 531 (Whyte 2001 In prep.). This represents a mean rate of increase of close to 50% per year which can only have occurred through immigration.

The rate of 6.6% which prevailed while the KNP population was entirely enclosed is probably a reflection of its natural performance. This is close to maximum and may be the result of culls holding the population at a level lower than that at which density dependent regulation might occur.

Lewis (1984) condcuted a ground survey in Luangwa National Park (Zambia) and found the proportion of calves of less than two years to be less than half of Hanks' study. He attributed this to a decrease in reproductive success, but as this study has shown, the conception rates may differ dramatically between years. Laws *et al.* (1975) have shown that east African populations have variable birth rates.

Calving interval

Calving interval plays the major role in driving the population changes. This was shown by the model of Whyte, van Aarde & Pimm (1998) and was a conclusion similar to that of

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Dobson (1993) and Hanks & McIntosh (1973). The MCI in rapidly expanding elephant populations has been reported at between 3.0 and 4.5 years but can be as low as 8 years (see Croze *et al.* 1981; Kerr 1978; Moss 1988; Smuts 1975; Williamson 1976, for a summary of these rates). The interval recorded in this study was 3.65 years, but when the data from Smuts (1975) are included, this increases to 4 years.

Calef used 3 years as the MCI in his model which yielded an estimate of 7% as the maximum rate of increase of an elephant population, but this seems too short. Moss (1988) found no evidence of a lactational suppression of oestrus as weaning of a calf occurred when the next calf was born. This means that the calving interval and age at weaning are the same. Moss found that calves of three years old found the weaning process difficult while at four the process was much easier. The KNP interval of 3.65 - 4.0 years agrees with Moss' observations. It is possible to record an MCI of 3 years or even less from pregnancy rates observed in a single year, but it seems highly unlikely that this could be sustained in the population over a period of many years.

Most of the other MCI's reported from elsewhere in Africa fall within the range of the annual MCI's recorded for KNP (Hanks 1972; Laws 1969; Laws & Parker 1968; Laws, Parker & Johnstone 1970; Lindeque 1988; Sherry 1975; Williamson 1976). The differences most likely result simply from the long gestation time and the calving interval itself. If a large proportion of cows in a population conceived in one year, this would influence the conception rates for the next three to four years. The recorded conception rate is thus partly dependent upon the recent history of conceptions in the population, and a sample based on a period of only three or four years may be subject to considerable bias. The MCI recorded by Smuts (1975) is almost certainly due to his study period coinciding with the end of the protracted droughts of the 1960's and early 1970's which were only finally broken in the rainy season of 1973/74 (see Figure 3). The inclusion of his results in the determination of the long-term MCI for KNP is thus important as they represent conditions which were not experienced during this study.

But droughts and the associated nutritional stress are known to have a greater affect on MCI. In Amboseli (Kenya) it exceeded six years during droughts (Moss 1988), and in Tsavo it

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was recorded at 6.8 years, and has been recorded at as much as 8 years (see Croze *et al.* 1981). This may be construed as a density dependent response to these conditions but the variation recorded for KNP suggests that it may be a response to prevailing environmental conditions, perhaps through nutritional stress. These occur during normal droughts and may affect an elephant population even at the low densities prevalent in KNP, though extremes such as those mentioned above have not been recorded. This in turn suggests that density dependent responses (as opposed to brief temporal responses to prevailing environmental conditions) may only begin to operate once habitats become degraded through over-utilisation. This is the important management concern – if the objective of reserve management is to maintain biodiversity, can we afford to wait for density dependence to regulate elephant populations?

Estimates of mortality rate

Various estimates of mortality in elephant populations have been made. These vary between 2.5 and 5% of the population dying each year (Laws & Parker 1968; Laws *et al.* 1975; Jachmann 1980; Dunham 1988 and references therein). The estimate of 3.2% obtained in KNP from the difference in the expected and observed rates of increase falls well within this range.

Whyte *et al.* (1998; see Chapter 6) derived an estimate for the mortality rate for KNP in a different way. They inferred the rate of increase by reasoning that "the consistent increases in the population when between 4 and 5% of the animals are killed makes 5% a reasonable estimate of the population's growth rate. Using the parameters of each cow calving first in their 12th year and at 3.6 years thereafter, the model estimated population growth at 6.5%. The difference between this and the estimated 5% growth rate, allows the calculation of annual mortality rate at 1.5%". This is 1.7% lower than the 3.2% estimated by the method used in this chapter, but the differences likely arise from the inferred approach of Whyte *et al.* (1998) while the estimate of 3.6% is derived from parameters measured directly from the population.

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CHAPTER 5: PART 3: ELEPHANT MOVEMENTS

INTRODUCTION

This section of the thesis was partially compiled from an earlier paper on elephant movement (Whyte 1993). Some of the findings of this paper are reviewed here, as data acquired subsequently suggest they were probably premature. As a result, an analysis of home ranges is included here with only a review of Whyte's (1993) interpretation of the effects of culls.

This study of elephant movements had its origin during culls. Culls were usually conducted in areas where numbers of elephants had concentrated, but reports were received from field staff engaged in culling operations that the elephants "disappeared" from areas where such culls had taken place, requiring long and costly helicopter searches to locate elephants for culls. Clearly some disturbances were associated with culls, but the actual cause of the disturbance was not known. It may have been the activities and sounds of the helicopter itself, or it may be that some form of "infra-sound" distress signals were emitted by animals being culled which disturbed other elephants in the vicinity. At the time it was realised that nothing was known of the movements of elephants in KNP. They may have been using the whole area of KNP rather randomly or else individual animals or clans may have occupied home ranges to which they confined themselves.

A further motivation for the movement study was that flight responses to culls might serve as a useful indicator of stress associated with these operations.

For the purposes of the management of this elephant population, the KNP was divided into four management regions (see Figure 1). Culling operations were conducted in only one of these regions each year. The question whether or not the culling programme induced movements across the regional (culling) boundaries in reaction to the culling programme was also raised. Should this have been the case, the practice of regional culling would have required reconsideration.

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This study was initiated using radio telemetry to address these questions, but due to the moratorium on culling imposed in 1995 (after the last culls conducted in 1994), the study on the impact of culls on movements was cut short.

Moss (1988) described the social structures amongst females and their young in the Amboseli National Park (Kenya) elephant population and these are summarised here as the are of relevance. The closest bond is between a mother and youngest calf, but these form part of a matriarchal group lead by the oldest female. She is the "grandmother", and all of her female offspring will remain with her for the rest of her life. This grouping is thus comprised of the matriarch, all of her mature daughters and all of their respective offspring. This grouping has very close bonds and remains almost permanently intact. Young males leave the group at around 14 years of age. This matriarchal group forms part of a wider structure known as the "bond group" which is comprised of matriarchal groups led by closely related matriarchs who will be either sisters or close cousins. These bond groups will often be in close proximity to one another and social ties are strong. The next level is the "clan". A clan is made up of related groups led by matriarchs who will probably be distant cousins. A close relationship also exists between bond groups of a clan who tend to occupy the same home range but may utilize the range independently of other bond groups. The next level is the "sub-population" made up of different clans. These tend to utilize neighbouring home ranges and the members of different clans may only be distantly related if at all. Finally the sub-populations collectively make up the "population".

These characteristics are also evident in KNP, but due to relative sizes of the population and the KNP, the individuals are not individually known. The relationships between the collared animals and those that they may be in association with are thus also not known.

Telemetry has become an almost essential tool in the study of animals, and various authors have reviewed techniques and problems. Handbooks have been published on the subject by Amlaner & Macdonald (1980) and Cheeseman & Mitson (1982) and a comprehensive

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review article was also published by Harris *et al.* (1990). Whyte (1996c) reviewed some of these techniques for use on elephants.

MATERIALS AND METHODS

Selection and distribution of collared animals

As an earlier elephant movement study in KNP had focussed on bulls (Hall-Martin In litt.[1]) this study was confined to the breeding herds. Adult cows were selected for deployment of the radio collars. Initially, the matriarch of the family group was selected for collaring, but as these are the oldest animals and as one mortality from old age occurred during the study, younger cows were selected in preference. Cows with very small calves at foot were also not selected.

Culling was conducted in only one of the four culling regions each year, so adult elephant cows were radio-collared a few months in advance of scheduled culls to determine home ranges and movements prior to the cull. At the initiation of the study in 1989, culls were scheduled for the far-northern region and seven cows were collared. In 1990 culling moved to the southern region and a further seven cows were collared. This was followed by seven cows collared in the central region in 1991 and another eight in the northern region in 1992. Due to two collar failures and three mortalities, a further five animals were collared in roughly the same areas where the original animals were marked.

Animals to be fitted with radio collars were selected at widely separated localities to ensure that different "clans" (Moss1988) were sampled. In only one instance were two animals intentionally marked from a single large group of elephants in the Shingwedzi area.

Equipment

A helicopter (Bell 206 Jet Ranger) was used to facilitate the location and capture of cows to be collared.

[1] Dr A.H. Hall-Martin, South African National Parks, Pretoria.

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Elephant cows were immobilised using 3 ml aluminium projectile syringes (darts) with a 7 mm "collared" needle which prevented dropping out and loss of the dart. Darts were manufactured by SANP. These were fired from a modified Astra 20gge shotgun, using the drug combination recommended by Raath (1993) – 12 mg of the analgesic etorphine hydrochloride (M99: Kruger-Med Pharmaceuticals (Pty.) Ltd.), and 100 mg of the neuroleptic tranquiliser Azaperone (Stresnil: Janssen Pharmaceutica). After recumbency, animals were fitted with the collar, which was placed around the neck behind the ears. The animals were revived using 24 mg of the antagonist Diprenorphine (M5050: Kruger-Med Pharmaceuticals (Pty.) Ltd.) delivered intravenously.

Transmitters were manufactured by "Telonics" and were standard VHF radio transmitters attached to a collar. These transmitters emit a pulsing signal on a predetermined frequency (148.000 – 149.999 MHz) which are detected on a radio receiver (also manufactured by Telonics) set to the same frequency. The signal is detected through a directional (Yagi) antenna attached to the receiver which in turn emits an audio signal through a speaker or headphones. The strongest signal is received when the antenna is directed straight at the transmitter.

Capture methods

The helicopter was used to search for study animals. As it could not be predicted where a group was to be found, no ground crew were used and due to the limitations of space in the helicopter, a crew of only three people conducted the fitting of collars. Once a suitable group had been located and the study animal selected, immobilization was achieved by darting the elephants from the helicopter at close range (< 10 m). Darts were placed in the rump area. The group was then manipulated by the pilot to keep the target animal in a suitably open area where the helicopter could be landed. Once the cow had become recumbent, the rest of her matriarchal group was driven off to a safe distance.

When immobilized, elephants should be manipulated into a position of lateral recumbency as sternal recumbency interferes with their breathing (Raath 1993). Study animals often went down in sternal recumbency and could not be pushed over into lateral

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recumbency due to the small crew. Fitting of the collar was conducted as hastily as possible, and no mortalities were experienced.

Tracking of collared elephants

Tracking was initially conducted from a vehicle on the ground, but this proved very inefficient as it was laborious and time consuming. Elephants have large home ranges and locating the collared animal wasted much time in searching for the initial "contact". On the ground, radio signals could rarely be received beyond a range of about 5 km, and study animals were often too far off the roads in thick bush to allow an approach. Their positions then had to be roughly estimated (fixed) by triangulation on maps. Triangulation has some inherent errors (Amlaner & MacDonald 1980; Whyte 1996b) but for the present study it was assumed that locations were accurate to within one square kilometre.

Aerial tracking proved far more efficient. In March 1991, after undergoing pilot training, ground tracking was no longer used. A Cessna 182 or Cessna 206 were used for aerial tracking. These aircraft were fitted with a Yagi antenna on each wing strut which were connected to the receiver on the inside of the aircraft. This allowed the selection of either or both of the antennae to determine the initial direction of the collared animal. By then turning towards the signal and adjusting the aircraft's course to maintain an equal signal strength from the two antennae, it was possible to fly straight toward the target animal until visual contact was made. The advantages of the aircraft were that even in remote, inaccessible areas, the study animals could be located and positions fixed more accurately than through triangulation. From altitudes of up to 6 000 feet above ground level, radio signals could be received from distances of up to 70 kilometers. This meant that all of the study animals in KNP could be located in a single six-hour flight.

Before the advent of Global Positioning System (GPS) technology, localities of collared animals were plotted directly on to maps and grid references were determined later on return to the office. Once the aircraft was fitted with a GPS, grid references were obtained from a "way point" directly off the instrument as the aircraft passed overhead the study animal.

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Data analyses

The data set analyzed here was collected between 1989 and 1996.

Some of the methods of home-range analysis are mathematically elegant and highlight core areas of the home range. This is useful in studies of resource utilization and activity patterns. One such analysis is the "Harmonic mean" (Dixon & Chapman 1980) which draws isopleths (like contour lines) defining the areas favoured. This is useful if sufficient geographically accurate fixes are obtained (such as can be obtained from GPS collars (Douglas-Hamilton 1998; Thouless 1996a) and from satellite collars (de Iongh *et al.* 1999; Lindeque & Lindeque 1991; Verlinden & Gavor 1998)), but when plots are obtained through the coarser methods like triangulation, they are less useful.

Tracking at regular time intervals allows meaningful comparisons of movements between data points and is useful for studies of home range and resource utilization (e.g. de Boer *et al.* 2000; Thouless 1995; Funston 1999; Lindeque & Lindeque 1991). Collection of movement data in this study was hampered through budgetary restrictions and an inability to track the study animals at regular intervals due to other work pressures. This resulted in an irregular tracking schedule which placed limitations on the analysis of the data. For this reason, only minimum convex polygons (MCP's) were used to analyze the data using the program CALHOME (Kie *et al.*1996). The program calculated the areas of the 100% MCP's which included all fixes, and also the 90% MCP's which excluded the outermost 10% of observations. These represent the occasional excursions from the main areas of the home ranges.

RESULTS

Home ranges

A total of 34 elephants were fitted with radio collars throughout KNP which were studied for varying lengths of time (see Table 12). Of these, 29 yielded more than 10 locality plots and allowed estimates of home range size. These home ranges are illustrated in Figures 16 and 17 and the number of fixes obtained for each animal with their respective 100% and 90% MCP's is given in Table 12.

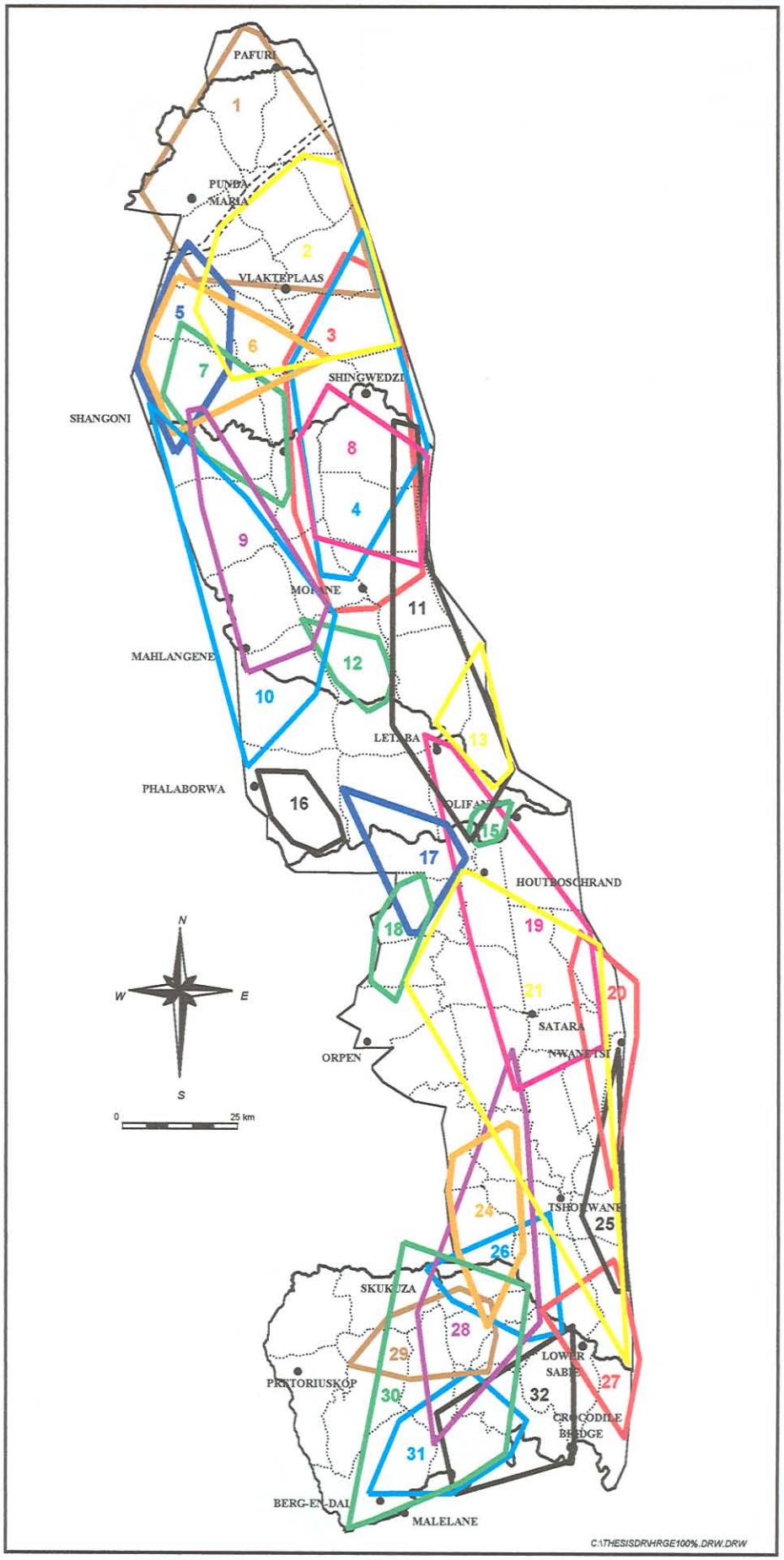


Figure 16: Minimum convex polygons (100% MCPs) showing the home ranges of 29 radio collared elephant cows in the Kruger National Park.

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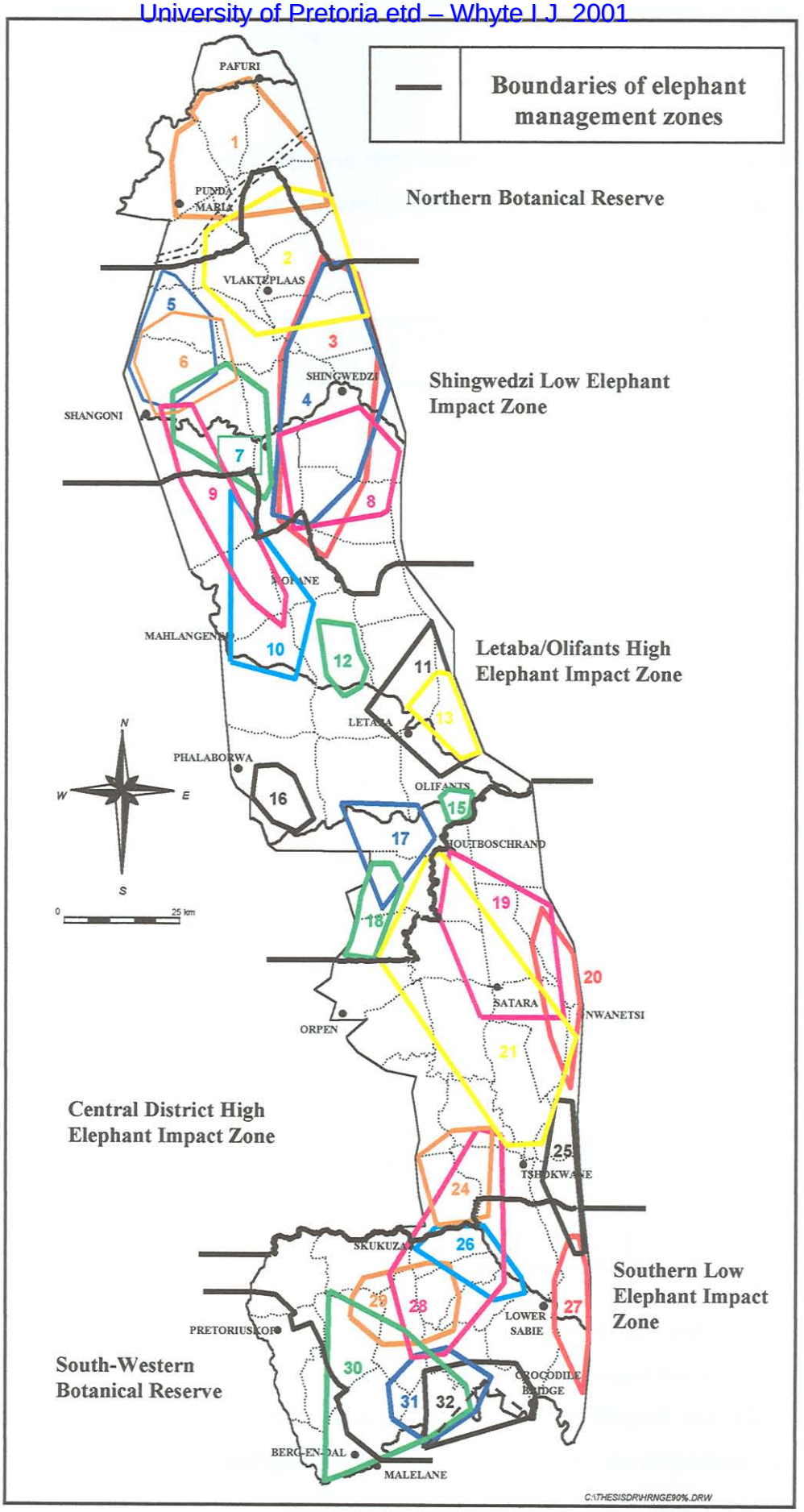


Figure 17: 90% MCPs of the home ranges of 29 radio collared elephant cows in KNP. Note how the boundaries of elephant management zones were defined on these home ranges.

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Table 12: Areas (in km^2) of 100% and 90% Minimum Convex Polygons (MCP's) defining the home ranges of 29 radio-collared elephant cows in the Kruger National Park tracked between 1989 and 1996.

Elephant No.	No. of fixes	Study period (months)	100% area (A)	90% area (B)	(B) as % of (A)
1	72	73	1337	748	56
2	75	58	1538	854	56
3	73	77	1567	984	63
4	63	61	1442	892	62
5	70	77	682	332	49
6	72	58	618	398	64
7	62	61	627	392	62
8	37	39	1127	611	54
9	30	39	1474	1041	71
10	16	39	562	381	68
11	25	39	1312	406	31
12	21	36	143	103	72
13	13	22	297	201	68
15	25	39	86	45	52
16	20	39	271	217	80
17	34	52	542	404	74
18	33	52	258	156	61
19	27	46	1061	760	72
20	34	52	589	317	54
21	31	46	2776	1805	65
24	16	12	671	394	59
25	32	52	379	266	70
26	61	55	540	174	32
27	32	51	513	201	39
28	51	61	1525	1096	72
29	56	42	558	368	66
30	30	57	1744	887	51
31	43	45	482	323	67
32	46	42	789	398	50

The recorded home ranges (100% MCP's) varied in size between 86 km^2 and 2 776 km^2 with a mean of 880 km^2 (S.D. = 1 154.6), while the 90% MCP's ranged from 45 km^2 to 1 805 km^2, with a mean of 523 km^2 (S.D. = 388.7). As the program excludes the outermost fixes in each of the polygons in the 90% MCP analysis, the proportion of the

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areas retained varies. These ranged from 31% to 80% with a mean of 60% (S.D. = 12.0) of the 100% MCP's.

There were large differences in home ranges sizes between respective study animals. This variation could be expected to reflect differences in the length of time respective animals were studied and the number of fixes obtained, but some of the ranges were large over a short period while others remained small (e.g. Nos 1, 15 and 21. See Figures 16 and 18). There was a poor linear relationship ($y = 337.6 + 4.47x$; $\mathbf{r} = 0.227$; $\mathbf{p} < 0.1$) between the number of fixes obtained and the respective areas of the 90% MCP's (Figure 19).

The 100% MCP's of neighbouring animals showed considerable overlap which was much reduced by the 90% MCP's. As emphasized by the CALHOME program (Kie, *et al.* 1996), the outlying points tend to represent excursions from the main area of the home range, and that by removing these from the analysis, a better picture of how neighbours utilize resources emerges. A visual comparison of Figures 16 and 17 shows the separation between the recorded ranges.

In the one instance where two animals were intentionally marked from a single large group of elephants (nos. 3 and 4 in the Shingwedzi area), their 100% MCP's show that different excursions were undertaken, but that the 90% MCP's were almost identical. They were thus almost certainly of the same clan. These two cows were recorded in the same group on three occasions, but were usually in different parts, even at opposite ends of their home range. Another animal (no. 8) was collared in the extreme southeast of her range and, but for collar failure, she may also have turned out to be of this same clan (Figure 16). Other animals marked at different localities were also found to share home ranges. Nos. 5 and 6 shared a range as did nos. 9 and 10, and both pairs were probably members of respective clans (Figure 16). These pairs were also recorded together at times but more often at separate localities within their home ranges.

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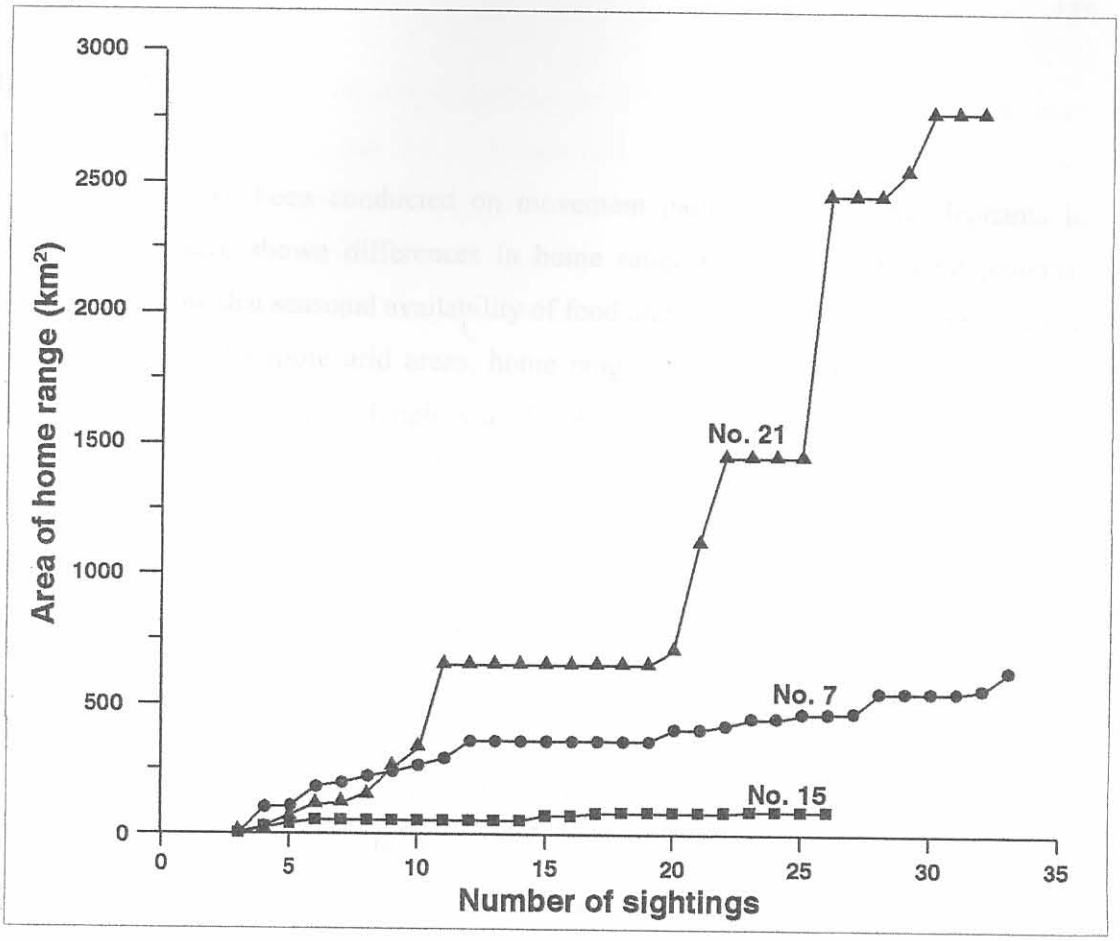


Figure 18: The relationship between the number of telemetry fixes and home range area of three selected radio-collared elephant cows in Kruger National Park (100% MCP's).

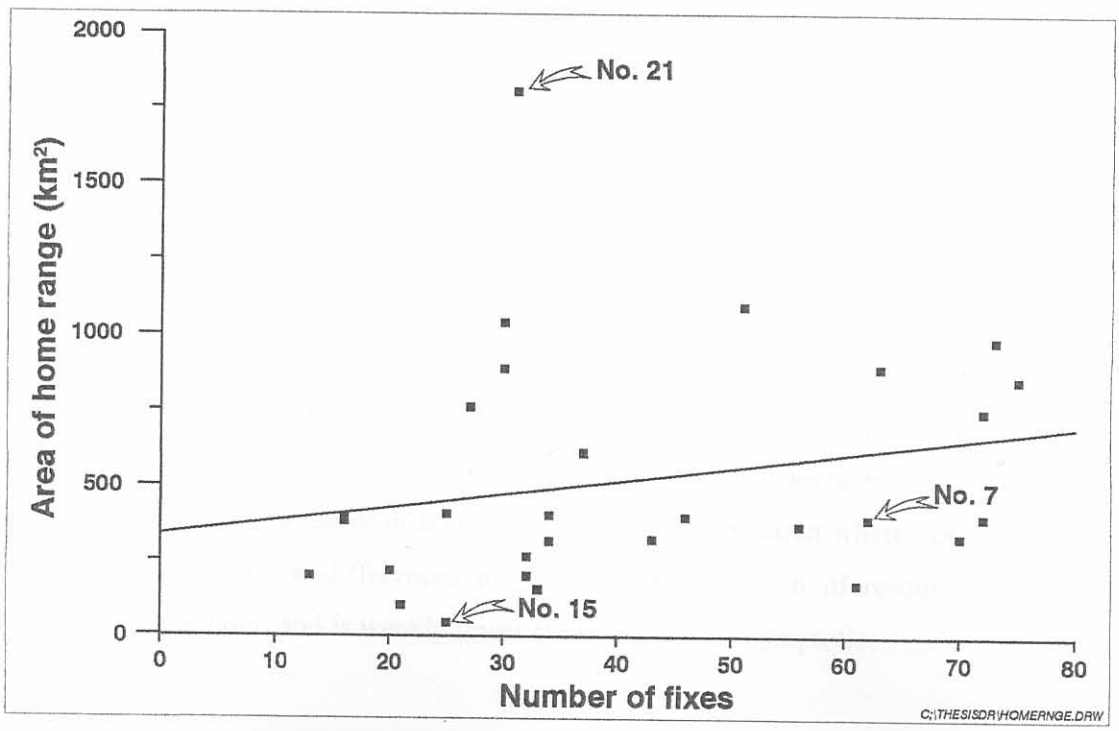


Figure 19: The relationship between the number of telemetry fixes and area of respective home ranges of radio-collared elephant cows in Kruger National Park (90% MCP's).

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DISCUSSION

Home ranges

Several studies have been conducted on movement patterns of savanna elephants in Africa. These have shown differences in home range sizes and movement patterns. These studies show that seasonal availability of food and water are the main determinants of movement. In the more arid areas, home ranges tend to be large and some show seasonal migratory patterns (de Iongh *et al.* 1999; Lindeque & Lindeque 1991; Thouless 1995, 1996b; Verlinden & Gavor 1998; Viljoen 1989). In more mesic areas these tend to be smaller and seasonal migrations are not evident (de Villiers & Kok 1997; Dunham 1986: Martin 1978). Data acquired for this home range study were collected over periods of up to six years. Until the end of the period covered, the study animals had remained in their defined home ranges, and thus conformed to the latter pattern.

The establishment of the network of artificial waterholes throughout KNP (see Joubert 1986) may have played a role on home range stability, but unlike Botswana (Verlinden & Gavor 1998) where the only permanent water is in the Chobe/Linyanti River in the dry season, KNP has a well distributed system of permanent and semi-permanent rivers and waterholes. Most of the collared elephants in this study had direct access to the permanent rivers within their home ranges, and those that did not would only have had to change their ranges in the worst of droughts to have gained access to these rivers. It is therefore unlikely that home ranges differ significantly now from what they may have been historically.

The relationship between the number of fixes and home range sizes in different animals in KNP was poor. This is reasonable because if an animal occupies a finite home range, the relationship between these two variables will be asymptotic, not linear (Thouless 1996a; Whyte 1996b; see Figure 18). A point is reached when increasing number of fixes no longer results in increases in home range size. In a population where home range sizes vary (probably due to differences in the spatial distribution of resources), this relationship does not hold, and is weakly linear (Figure 19), not asymptotic.

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The large home ranges of some of the elephant cows tracked are in some contrast to most of the others. Although this may be an entirely natural phenomenon, there may be other reasons for this. One of the cows (no. 21 in the Central Region) had the largest recorded range of all and on one occasion when her collar was replaced, she was found entirely on her own, with no other elephants in sight. On no other occasion were any of the collared animals recorded on their own. This was thus highly unusual (Moss 1988) and the possibility exists that she was not a member of a matriarchal group, and that the large home range was the result of wandering between groups. Tracking from the air makes it impossible to recognize individual animals and so it is not known whether the animals she was accompanying were always the same. Speculation suggests that her matriarchal group may have been culled prior to the collar being fitted, and that culling may thus play an unsuspected role in the determination of some animals' movements.

The distinct home ranges (90% MCP's) of the collared cows suggest that the social structures as described by Moss (1988) apply also to the KNP population. It is not known how many elephants or matriarchal groups may constitute a "clan", or whether the movements of the collared cows is representative of the clans, but the almost identical 90% MCP's of collared cows sharing home ranges strongly suggest that they are. Moss (1988) suggested that aggressive interactions between clans may exclude neighbouring clans from each others' home ranges, but that confirmation was required through further research. If Moss' suggestion is correct, this would explain why the clans in KNP (as represented by the collared cows) do show distinct home ranges.

Home ranges of 11 of the collared elephants spanned the boundaries of the old culling zones which were arbitrarily designated along the KNP's rivers (Joubert 1986). While these boundaries may have served a useful management purpose, they presented no barriers to elephant movement which complicated the analysis of sub-population trends (van Aarde *et al.* 1999; see Chapter 6).

In the proposed new policy for the management of the KNP's elephant population (Whyte *et al.* 1997; Whyte *et al.* 1999; see Chapter 7), the boundaries of the elephant management

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zones were designated on the known boundaries of home ranges of the collared cows presented here (see Figure 17). It is hoped that the fidelity shown to home range so far will persist once culls begin and limit movements between the zones. But this "fidelity" may be nothing more than exclusion through aggression by neighbours. Should elephant numbers decline in the "low elephant-impact zones" as prescribed in the new policy, these levels of aggression may also decline, resulting in less inhibited movements out of the "high elephant-impact zones". This would be completely contrary to the objectives of the policy as low elephant numbers would not be attainable in the low impact zones and neither would high numbers be reached in the high impact zones. A source-sink situation would develop requiring the killing of large numbers of elephants without the objectives of the policy ever being achieved. On the other hand, the disturbance of active culling might in itself deter movements out of the high impact zones. This seems more likely in which case movements will go the other way – from the low- into the high impact zones. This will facilitate the policy as the objectives of high and low numbers in the respective zones will be achieved sooner.

Movements in response to culls

While Whyte (1993) drew some conclusions on the effects of culls on collared animals, the results were not included here as the statistical analysis of the data and interpretation of the results were prejudiced by the fact that the collection of data was sporadic. The problems associated with the data were that movement data collected prior and subsequent to culls were not collected at regular time intervals. This means that movements recorded may have been a function of time rather than disturbance. Also, the distances between collared and culled animals were not accurately determined at the time of the cull, and could have varied from a few hundred metres to several kilometres. The "flight stimulus" was thus not known or measurable. Finally, the relationships between culled and collared animals were not known. While this may have been impossible to establish without long-term observational studies, such relationships may have influenced movements either way. If the matriarch was culled and some of her matriarchal group not, they may have remained in the area having been rendered leaderless, but members of a group from a more distant relationship may be less restrained in their flight response. A

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conclusion that no movement subsequent to a cull implies minimal stress may thus be incorrect.

CONCLUSIONS

The elephants of KNP are non-migratory and show a high degree of fidelity to their home ranges. Home range sizes are variable in size which is probably due to the abundance and spatial distribution of resources.

The initial conclusion of Whyte (1993) that culls had induced movement out of an animal's normal home range was premature as the full extent of the study animals' home ranges had not been determined. The movements recorded at that time took the animals outside of their known home ranges, but the longer study has now shown that home ranges are larger than thought and that they returned to these "flight" areas even when not under the stress of culls. The conclusion drawn with later insights would have been that while culling may have induced some movements, these did not induce the affected elephants to move out of their normal home ranges.

Due to home ranges spanning the boundaries of the old culling zones, sub-population trends would have been influenced by movements between sub-populations rather than changes in density dependent demographic variables. This complicated the analysis of trends (van Aarde *et al.* 1999) and if a similar culling program should be initiated in future, greater cognizance of home range boundaries should be taken when defining management compartments.

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CHAPTER 5: PART 4: CULLING AND THE DYNAMICS OF THE POPULATION

INTRODUCTION

Part 4 of this chapter was compiled from the paper by van Aarde *et al.* (1999).

For thirty years, managers have promoted culling as a management tool for African elephant populations confined to areas set aside for conservation (e.g. Buechner, *et al.* 1963; Glover, 1963; Joubert 1986). Based on the findings of Van Wyk & Fairall (1969), the Board of South African National Parks initiated a programme of elephant culling in 1967 to maintain the KNP population at about 7 000 individuals (0.32 elephants per km^2). This was a measure to prevent the anticipated destruction of the vegetation in KNP. That decision resulted in the culling or live removal of 16 520 elephants from KNP between 1967 and 2000. Increasing public pressure and the lack of published proof of the ecological damage caused by high elephant densities in KNP resulted in SANP agreeing in 1995 to temporarily suspend culling until the policy could be reviewed (see Chapter 7). However, Cumming *et al.* (1997 and references therein) and others such as Western & Gichohi (1989) have demonstrated how high densities may dramatically reduce biological diversity. The "elephants versus biodiversity" debate remains controversial.

Annual aerial surveys provided the information for the determination of culling quotas to keep elephant densities within the suggested range (Joubert 1986). From 1967 to 1984 elephants were culled from areas throughout the KNP. However, from 1985 to 1994, KNP staff identified four management regions separated by rivers and which covered the park's entire area (Figure 1). The total quota for a given year came from only one of these regions and it removed from 6 to 32% of the local population.

This section of the thesis examines the response of elephants to culling by determining how post-culling densities affected population growth rate. The analyses suggest there may be an alternative management strategy for the elephants in KNP. Left alone, high densities of elephants may decline (e.g. Moss 1988) so there may be cases where human intervention is not necessary.

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MATERIALS AND METHODS

Culling

Culling methods and quotas are given in Part 2 of this chapter. Between 1967 and 1984, culls took place throughout the KNP, but from 1984 to 1994, the total quota each year was removed from one of the four management regions. In practice, this resulted in a three to five year period between culls of a population of a given region. As a result of this, and of the discontinuation of the culling programme since 1995, a specific region experienced from one to seven years of no disruption by culling after a specific cull. Each of these regions is referred to as a sub-population.

Data analyses

Density dependent mortality suggests that there is a population density, K, below which densities X_t in year t, tend to increase to the following year (t+1) and above which they tend to decrease, i.e.

$$\text{When } X_t < K,\ X_{t+1} - X_t > 0 \text{ and when } X_t > K,\ X_{t+1} - X_t < 0$$

The year-to-year change in population density, $X_{t+1} - X_t$ has been called D. The null hypothesis of no density dependence suggests a population model:

$$X_{t+1} = X_t + \sigma$$

where σ is random variation. Under the null hypothesis $\mathbf{D} = \sigma$. Based on van Aarde *et al.* (1999) such a population follows a one-dimensional Brownian walk over time and the variance of population size constantly increases.

It may be expected that linear regression of D against initial density X_t should not reject the null hypothesis of this model. Were D to decline significantly as X_t increases, the null hypothesis would be rejected, density dependence would be accepted and the value of X_t where $D = 0$ would be used as an estimate of K. The method seems reasonable, but is

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statistically flawed. The method uses $X_{t+1} - X_t$ $(=D)$ as the dependent variable and X_t as the independent variable. By this use, they are obviously dependent on each other. This is not new in population ecology, but a different approach has been used.

The flaw is that population densities are measured with error. A serious accidental underestimate of the true density in one year will lead *simultaneously* to a low value of X_t and corresponding high value of D. Consequently, regressions of population change (D) against initial population density X_t show strong, spuriously significant negative correlations by chance alone when sampling error is large relative to the actual population changes.

The sampling error (precision) for the censuses of elephants in KNP is small (< 5%), while the numbers fluctuate by many hundred animals from one year to the next in a population of approximately seven thousand. This scenario was simulated with population sizes, fluctuations, and sampling errors broadly similar to what are observed. These simulations still show the spurious negative correlation of population change against initial population size. The spurious effect is small, however. (The percentage of variance explained by regressions of D versus X_t is never more than five percent and usually much less.) In the actual data, when a low density is followed by a population increase, then both the low density and the subsequent increase are real.

The flaw arising from the dependence on estimates of consecutive population densities is further weakened, because in one out of four years, the initial population estimate is that after the cull and not the previous year's value. Culls act as experimental interventions, allowing an answer to the question: to what extent does a population increase subsequent to a reduction in the population density to some prescribed lower level? Simply, the low post-cull densities are known to be real ones, not sampling artefacts.

It is believed that the data can be analysed in the way outlined above. Linear regression analyses of D against post-culling densities are used. The method has small flaws, but it

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is contended that these will not obscure the general results and that it has the advantage of being simple and intuitive.

RESULTS

Population growth

Culling did not halt elephant population growth in KNP, which fluctuated between 6 586 and 8 821 animals. Successive years of decrease in numbers were followed by successive years of increase in numbers (Figure 20). The fraction of the total population removed through culling during a given year ranged from 0.2% to 20.9%. Expressed as a fraction of the sub-population affected by a given cull from the values ranged from 5.9 to 31.6%.

Table 13 presents the annual population density before the cull, the density of elephants culled, ***C***, and from their difference, the population density after the cull. It then displays on the same row the pre-cull density of the following year and from them calculates the change in population density. Annual counts were in August/September of year ***t*** while culling took place between April and June of year ***t+1***. Entries of these values in the same rows facilitate further calculations. Pre-cull densities ranged from 0.221 to 0.552 elephants/km^2, with a mean value of 0.339 (±0.009) elephants/km^2. Post-cull densities during the period of culling ranged from 0.198 to 0.400 elephants/km^2, with a mean value of 0.307 (±0.007). Annual growth rates expressed as yearly differences in post-cull densities in year ***t*** and pre-cull densities in year ***t+1*** ranged from -0.13 to +15.8 (see Table 13).

Density dependence

Population growth rate, ***D***, decreased significantly with an increase in post-cull density (Figure 21; Table 14). Population densities above 0.37 elephants/km^2 usually declined during the next year when not culled. However, there were exceptions. The North sub-population, increased from a density of 0.37 in 1995 to 0.39 (1996), 0.40 (1997) and 0.48 (1998). The South sub-population's density increased from 0.36 in 1994 to 0.45 (1995),

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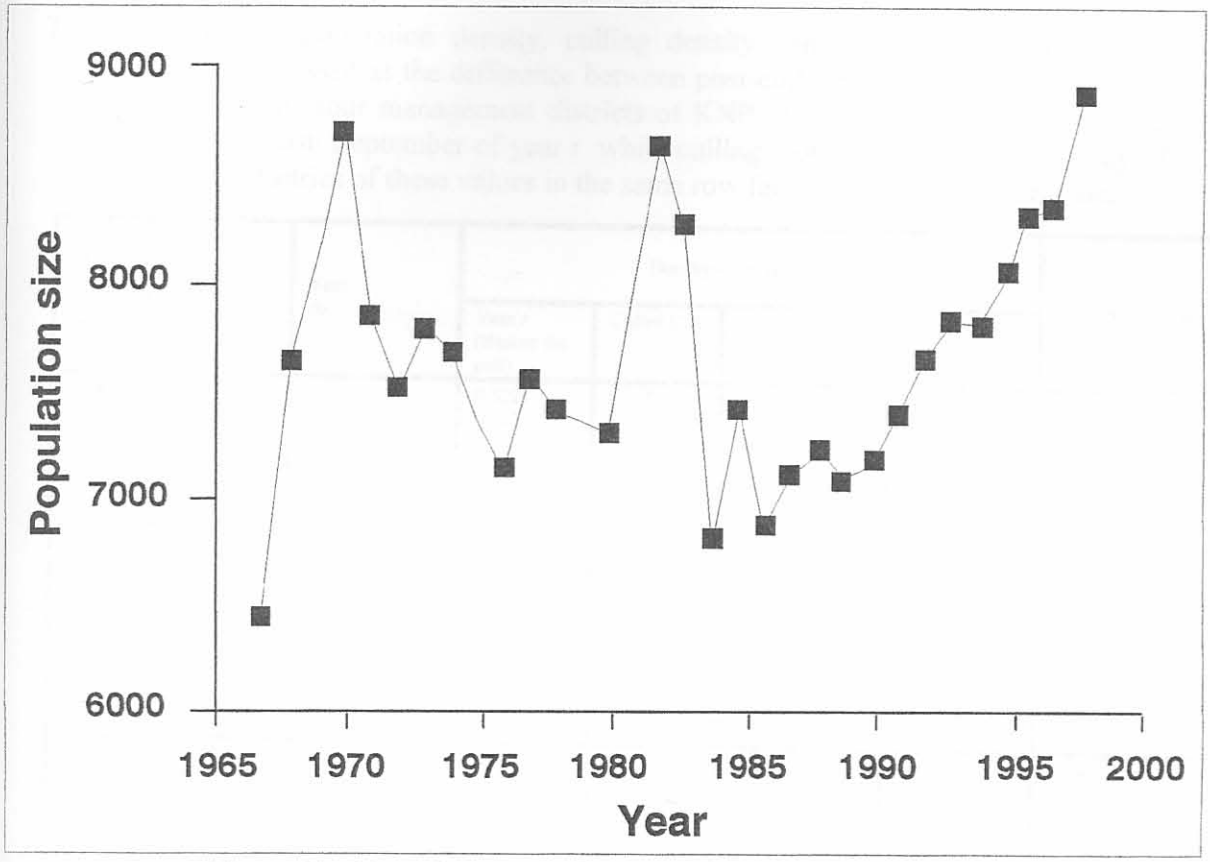


Figure 20: Trend in the total population size for African elephants in the KNP based on aerial surveys conducted annually between 1967 and 1998. The population was exposed to culling as a management option from 1967 to 1994.

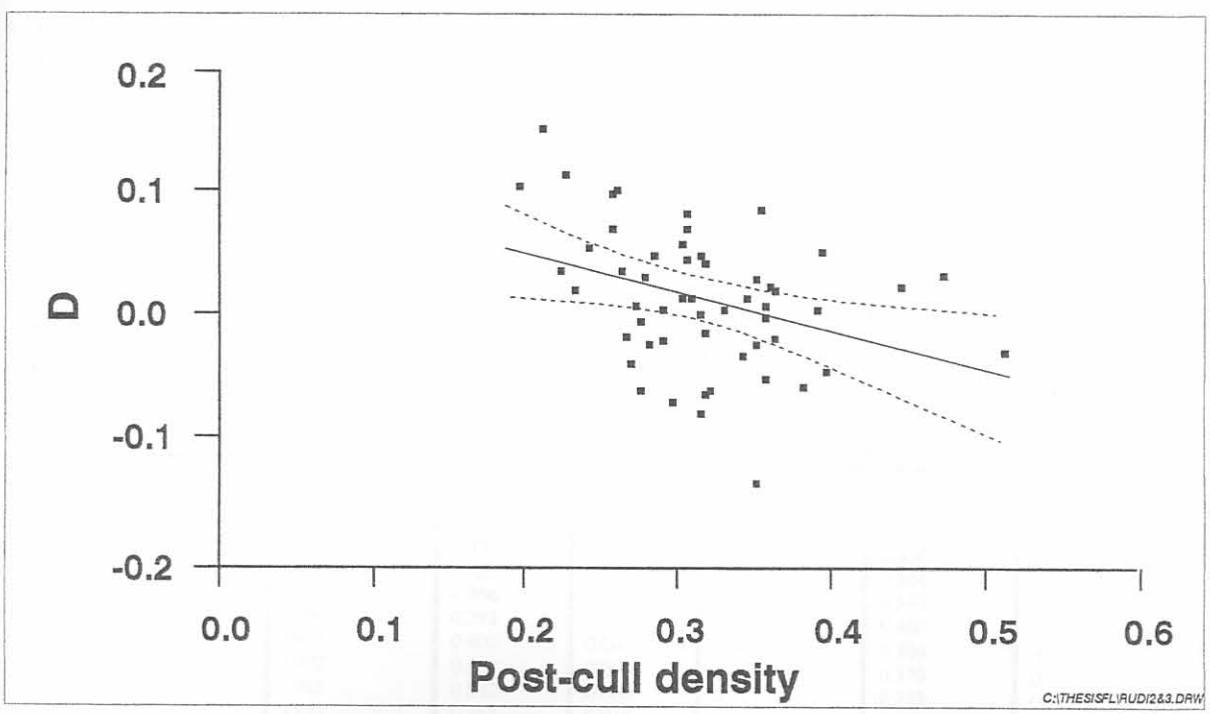


Figure 21: The relationship between change in population density (D) and post-cull density for all sub-populations of African elephants in the KNP.

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Table 13: Annual population density, culling density and change in population density expressed as the difference between post-cull density and the density after a cull for the four management districts of KNP. Annual counts were conducted during August/ September of year *t* while culling took place during April/May of year *t+1*. Entries of these values in the same row facilitated further calculations.

Management District (area)	Year *(t)*	Density (elephants km^{-2})				Change in density, D
		Year *t* (Before the cull)	Culled C_t	Year *t* (Post cull)	Year *t+1* (After the cull)	
Far North (4 190 km^2)	1984	0.522	0.165	0.357	0.227	-0.130
	1985	0.227	0.000	0.227	0.268	0.041
	1986	0.268	0.000	0.268	0.237	-0.031
	1987	0.237	0.000	0.237	0.264	0.026
	1988	0.264	0.000	0.264	0.372	0.108
	1989	0.372	0.074	0.298	0.232	-0.066
	1990	0.232	0.000	0.232	0.346	0.114
	1991	0.346	0.000	0.346	0.363	0.018
	1992	0.363	0.000	0.363	0.351	-0.012
	1993	0.351	0.062	0.289	0.298	0.009
	1994	0.298	0.010	0.289	0.275	-0.014
	1995	0.275	0.000	0.275	0.284	0.009
	1996	0.284	0.000	0.284	0.267	-0.016
	1997	0.267	0.000	0.267	0.308	0.041
	1998	0.308	0.000	0.308	-	
North (5 980 km^2)	1984	0.324	0.035	0.289	0.335	0.047
	1985	0.335	0.020	0.316	0.308	-0.008
	1986	0.308	0.000	0.308	0.359	0.051
	1987	0.359	0.000	0.359	0.362	0.003
	1988	0.362	0.046	0.316	0.257	-0.059
	1989	0.257	0.000	0.257	0.358	0.101
	1990	0.358	0.000	0.358	0.312	-0.045
	1991	0.312	0.000	0.312	0.330	0.017
	1992	0.330	0.051	0.279	0.281	0.002
	1993	0.281	0.000	0.281	0.317	0.036
	1994	0.317	0.000	0.317	0.369	0.053
	1995	0.369	0.000	0.369	0.392	0.022
	1996	0.392	0.000	0.392	0.401	0.009
	1997	0.401	0.000	0.401	0.458	0.057
	1998	0.458	0.000	0.458	-	
Central (5 475 km^2	1984	0.342	0.022	0.320	0.354	0.034
	1985	0.354	0.000	0.354	0.389	0.035
	1986	0.389	0.070	0.319	0.245	-0.075
	1987	0.245	0.000	0.245	0.303	0.058
	1988	0.303	0.000	0.303	0.322	0.019
	1989	0.322	0.000	0.322	0.266	-0.056
	1990	0.266	0.000	0.266	0.256	-0.011
	1991	0.256	0.057	0.198	0.304	0.105
	1992	0.304	0.000	0.304	0.365	0.061
	1993	0.365	0.000	0.365	0.352	-0.013
	1994	0.352	0.000	0.352	0.333	-0.019
	1995	0.333	0.000	0.333	0.341	0.009
	1996	0.341	0.000	0.341	0.315	-0.027
	1997	0.315	0.000	0.315	0.322	0.007
	1998	0.322	0.000	0.322		
South (3 840km^2)	1984	0.326	.0490	0.277	0.221	-0.056
	1985	0.221	0.000	0.221	0.379	0.158
	1986	0.379	0.000	0.379	0.326	-0.053
	1987	0.326	0.066	0.260	0.330	0.071
	1988	0.330	0.009	0.322	0.366	0.045
	1989	0.366	0.000	0.366	0.393	0.027
	1990	0.393	0.081	0.312	0.400	0.088
	1991	0.400	0.000	0.400	0.360	-0.041
	1992	0.360	0.000	0.360	0.370	0.011
	1993	0.370	0.060	0.311	0.393	0.082
	1994	0.393	0.033	0.360	0.449	0.090
	1995	0.449	0.000	0.449	0.477	0.027
	1996	0.477	0.000	0.477	0.514	0.037
	1997	0.514	0.000	0.514	0.485	-0.029
	1998	0.485	0.000	0.485		

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0.48 (1996), and 0.51 (1997) before declining again. There is evidence for density dependence, but it is a far from perfect regulator for those who must consider the long-term consequences to the KNP's vegetation.

The simple regression technique readily allows further statistical exploration. Firstly, the question can be asked: Do the four regions differ in their degree of density dependence? The slopes of the lines describing the above relationship for each of the management areas did not differ significantly from each other ($F = 1.029$; df 3 & 48; $p=0.388$). This analysis of covariance shows that the four regions were homogenous and the density intercept for all districts combined suggests inhibition of growth at a density of 0.374 elephants/km^2 (Table 14).

Table 14: Linear regression variables for the relationship between change in population density and post cull density for elephant sub-populations in KNP as presented in Table 13. (* denotes $P<0.01$)

District	Slope	Y-intercept	X-intercept	r^2	F-value for deviation of slope from zero
Far North	-0.900±0.324	0.264±0.093	0.293	0.392	7.728*
North	-0.267±0.265	0.107±0.087	0.402	0.078	1.016
Central	-0.625±0.242	0.206±0.076	0.324	0.356	6.644*
South	-0.374±0.189	0.119±0.037	0.445	0.246	3.909
All districts	-0.317±0.113	0.167±0.069	0.374	0.128	7.940*

Statistically, no more should be seen in the slopes and intercepts of these regional analyses. However, managers might see the differences between them supporting independent observations. Table 14 shows the regional results for this purpose. Only the regressions for the Far North and Central regions differed significantly from zero (see Table 14), tentatively suggesting that density dependence may be more powerful here. The density-intercepts for the four regions ranged from 0.293 to 0.445, suggesting that there might be regional differences in the density at which growth may be inhibited (Table 14).

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Secondly, what is the impact of the cull itself? The residuals about the ***D*** versus post-cull density plots can themselves be plotted against culling density. The residuals decrease as culling intensity increases (Figure 22), suggesting that culling intensity does affect population changes. An analysis of the influence of culling on population change showed that population change was affected by the time that elapsed since the cull. Figure 23 plots the residuals of population change verus post-cull density, against the number of years that have elapsed since culling. Culling was followed by a sharp relative decrease in the rate of change in the year following a cull (Figure 23). Mean values two and three years after the cull were higher.

The simplest interpretation of Figure 23 is that relative to the expected density change, populations tend to be smaller than expected in the year immediately after the cull and to recover the following year. It seems likely that elephants initially move *out* of regions where other elephants have been killed, not *in* as would be expected if they responded solely to the increased availability of resources. This behavioural effect makes culling seem more effective than it is.

DISCUSSION

Culling raises ethical, social, and economic problems (see Cumming *et al.* 1997; Butler, 1998; Whyte *et al.* 1998). SANP strives to maintain biodiversity and thus seeks ways of preventing the losses through habitat destruction. The culling of elephants from 1967 to 1994 kept the population at between 7 000 and 8 500 individuals (see Figure 20) and thus within their stated limits of accepted influence on their environment in KNP as stated in their management plan (Joubert 1986).

The obvious questions are; was this the right range of population densities, and was the management plan the best way to achieve that range?

Was the range of densities correct?

The practice of limiting culling to a given area, followed by a number of years of no culling in that area, provided the opportunity to assess the response of sub-populations to

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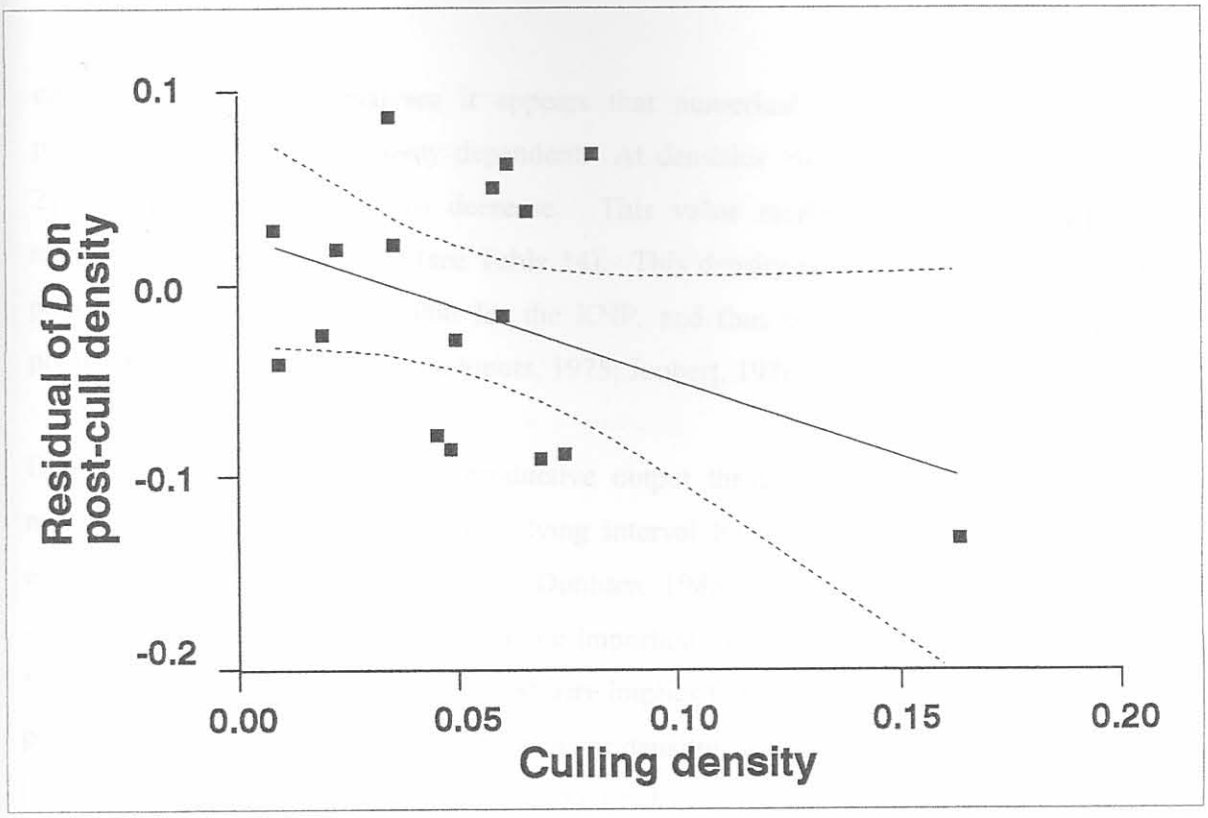


Figure 22: The relationship between the residuals of *D* on post-cull density and culling density described by a linear regression line with the equation $y = 0.0357 - 0.759x$ ($r = 0.173$).

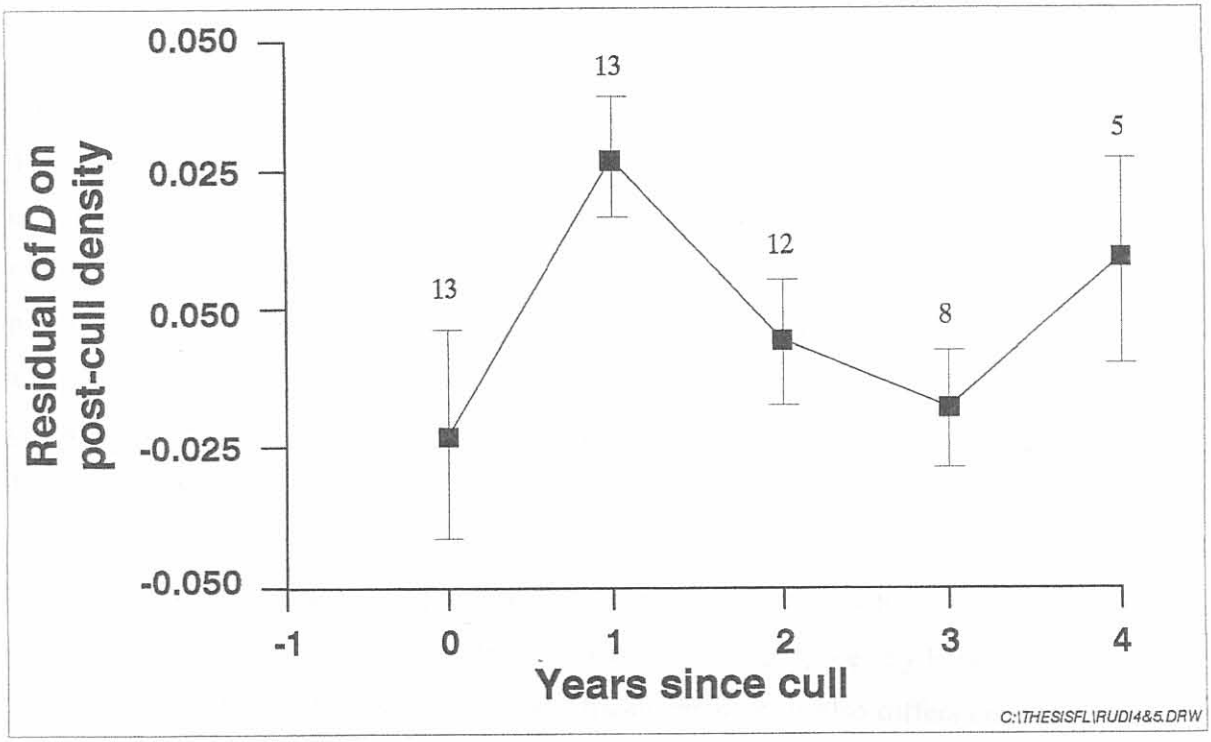


Figure 23: The influence of culling on population change expressed as the mean values of *D* on post-cull density against the number of years that have elapsed since culling. The above the standard error bars denote sample size.

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culling. From these analyses it appears that numerical changes in elephant sub-populations in KNP are density dependent. At densities >0.374 elephants/km^2 (Figure 21) the population tended to decrease. This value might differ for the different management regions of KNP (see Table 14). This density is equivalent to an elephant population of very nearly 8 000 for the KNP, and thus within the limits set for the population by park managers (see Smuts, 1975; Joubert, 1986).

Density induced regulation of reproductive output through changes in age at sexual maturity, pregnancy rates and inter-calving interval have been recorded for elephants elsewhere in Africa (see Laws, 1969; Dunham, 1988 ; Dobson, 1993, and references therein). Such density dependence may be important in population regulation (Hanks & McIntosh, 1973). The analysis presented here implies that in KNP density dependence of population growth rate only starts operating at densities greater than 0.37 elephants/km^2. In terms of the total KNP it is of interest to note that such a density was only achieved in 1970. Until 1995 densities have been maintained at values ranging from 0.31 to 0.40 elephants/km^2.

Van Jaarsveld *et al.* (1999) found no evidence for density dependent effects in South African elephant populations, with a mean density of 0.33 elephants/km^2 (Hall-Martin 1992). This conclusion matches those from the analyses presented here. The suggestion of Smuts (1975) that a density of 0.4 elephants/km^2 still had no regulatory effect on reproduction does not agree with these analyses, since the inhibition of population change presumably results from differences between birth and death rates. However, these analyses were conducted on the sub-population level and changes in population size for a given region may have resulted from intra-population movements rather than changes in demographic variables.

The value of 0.37 elephants/km^2 proposed here as the density at which population growth rate is depressed is very much lower than the value of 0.57 proposed by Fowler & Smith (1973) as an "equilibrium" density for the African elephant. It also differs considerably

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from the value of 1.19 elephants/km^2 suggested by Armbruster and Lande (1993) as an equilibrium value for elephants in semi-arid regions.

These higher values however are very similar to the equilibrium density estimated by Laws (1969) for Tsavo in East Africa. The discrepancy between this study's value and those mentioned above may be due to differences in habitat quality or due to the effect of long term management (culling) of KNP's elephants.

In summary, comparisons of studies elsewhere do not sensibly inform management within KNP. There may be differences of opinion about what is a reasonable density, but it seems more likely that there are real, underlying differences in ecology. What this study suggests is that densities in KNP will tend to be regulated around 0.37 elephants/km^2.

What does this value mean? Habitat deterioration associated with densities slightly higher than the value of 0.37 elephants/km^2 in KNP is of concern and implies that the present conservation paradigm (maintenance of biological diversity) requires some management action when elephant densities exceed the value of 0.37. Indeed, efforts to maintain the population substantially below this level - at 7 000 to 7 500 individuals - were based on Van Wyk & Fairall's (1969) suggestion that densities of elephant >0.29 individuals/km^2 would result in the destruction of vegetation around water points.

Surveys have illustrated that widespread scarring of trees in the KNP by elephants only commenced during 1973 (Coetzee *et al.* 1979) when densities were at the level of expected density dependent feedback. Densities above 0.37 have occurred since 1995 in two sub-populations and habitat damage has been continuing ever since (personal observations). Thus, maintaining the population at a level where density dependent effects are apparent may cause habitat destruction.

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Are culls necessary?

When densities exceeded 0.37 elephants/km^2 they typically declined the following year when not culled. Thus, the strategy of culling immediately after high densities may have been premature. A wait of another year may have resulted in the population declining without such controversial intervention.

Moreover, the effectiveness of culls was often spurious. The immediate response of sub-populations of elephants to the cull was that of a local *decrease* in numbers, followed by a dramatic increase in population growth rate. The rates of increase recorded in response to culling (Table 13) often exceeded the maximum rate of increase of 7% estimated by Calef (1988) for the species. This implies that the calculated response of sub-populations to culling results not from an immediate increase in birth rate or a decrease in calving intervals, but rather from inter sub-population immigration, with "vacancies" created through the culling of sub-populations being occupied by members of neighbouring sub-populations. Thus, culling of a given sub-population may reduce environmental pressures exerted on neighbouring areas, while increasing that on the areas occupied by the culled sub-population. This outcome was not considered by KNP managers, as the intention of culls was to reduce overall elephant densities, but the consequences such fluctuations in the disturbances brought about by elephant may have for local diversity requires further investigation.

Can culls be eliminated entirely? Even though the analyses show that at densities >0.37 elephants/km^2 the killing of elephants may often be unnecessary, high densities have persisted for several years. It is not known if the vegetation of KNP can withstand such high densities. With densities presently exceeding the maximum values stipulated (Joubert 1986) for both the Southern and Northern management regions (see Table 14), vegetation changes in these regions need to be monitored.

In summary, the management recommendations are simple. It is known that the new elephant policy (Whyte *et. al* 1998; see Chapter 7) will not manage the population in the same way. However, policies are not cast in stone and a return to one similar to Joubert

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(1986) is not inconceivable. Culls should be considered only if a high elephant density persists for two or more consecutive years. They should not be an immediate response to high densities because typically such densities decline without intervention. The effects of persistent high densities on vegetation must be measured.

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CHAPTER 6: THE POST CULLING ERA (1995-1999)

PRELUDE

This chapter has been structured into two parts, each of which was compiled from a published paper which examined elephant management issues after the moratorium had been placed on the culling of elephants in 1995. The first of these two papers (Part 1) focused on the broader issues of the management of elephants and models the logistics of implementing a contraception programme (Whyte *et al.* 1998), and gives a brief overview of the local and global dilemmas of managing elephants. Part 2 examines management concerns surrounding the two contraception techniques which have received research attention in the KNP and their potential as a means of managing elephant (Whyte & Grobler, 1997).

Although a moratorium had been placed on the culling of elephants in 1995, this did not mean that SANP had altered its opinion on the necessity of limiting elephant numbers in confined national parks. The process of developing a new management policy (see next chapter) and inability to implement population limiting management, brought the dilemmas into clearer focus. These dilemmas were examined by Whyte (2001 In press).

Post moratorium, SANP maintained its right to manage the KNP population through non-lethal means. It developed its capacity to translocate elephants of all sizes and encouraged research in contraception techniques. Although Fayrer-Hosken *et al.* (2000) suggested that porcine zona pellucida (pZP) immunocontraceptive vaccine is a practical tool for controlling elephant populations, the technology is not yet considered to be logistically at a level where it can be used to control large elephant populations (Whyte & Grobler 1997; Whyte *et al.* 1998). However, SANP may continue supporting research that may lead to an ethically acceptable alternative to culling.

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CHAPTER 6: PART 1:
MANAGING THE ELEPHANTS OF THE KRUGER NATIONAL PARK

INTRODUCTION

Dilemmas of elephant management

The problems of managing the elephant population in KNP (and in most of southern Africa) are different from those of most of the rest of Africa. On the continental scale, space previously available to elephants is increasingly being occupied by Africa's burgeoning human population (Parker & Graham, 1989; personal observations) and elephant populations have suffered major declines due to excessive illegal killing for their ivory (Barnes *et al.* 1998). Yet within southern African countries, the opposite has been true – here many conservation areas have too many elephants. In KNP, over the last three decades, culls removed an average of 7% of the population per year (up to 1 800 animals in a single year). Without such intervention, the numbers might have doubled in as little as ten years (see Chapter 5: Calef 1988).

Experiences in a variety of relatively dry landscapes show that high numbers of elephants can change species-rich woodlands to species-poorer grasslands (see Cumming *et al.*, 1997; Western & Gichohi 1989). Until 1994, when a moratorium was placed on culling, the policy had been to prevent such changes through the limiting of the elephant population (Joubert, 1986). Management interventions that prevent nature from taking its course (such as elephant culling) will always be controversial, as they raise social and economic issues that transcend national parks' boundaries. This further constrains management options and leads to yet more controversy (Sugg & Kreuter 1994).

Another view is that income from elephant products and hunting might benefit local people living next to KNP, some of whom make only a subsistence living (Bond 1994). Such income might engender a view of the elephant as a resource, rather than a competitor, but such local actions may have unintended global consequences (Hutton & Chitsike 1999). Across most of Africa, elephants are in a rapid decline, usually attributed to poaching and the illegal ivory trade (Lewis, 1984; Douglas-Hamilton, 1987; Barnes & Kapela, 1991; Caughley *et al.* 1990). It has been suggested by some who oppose the trade in elephant

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products that selling ivory where elephant populations are protected and increasing creates an unregulated market that will probably lead to poaching and possible subsequent extinction elsewhere (Kenya Wildlife Service 2000).

Ethical issues also compound elephant management problems. Many people, including those who might never visit the KNP, object to the killing of large wild mammals which may have economic consequences. Tourists who visit national parks may feel offended that the animals they have travelled so far to see are locally considered pests and shot. Tourist boycotts or unwillingness to visit such national parks as a consequence might lead to a loss of revenue. Hunting is another management option which could yield considerable revenue (Bond 1994), but finding common ground between those for whom hunting is a passion and for those who passionately oppose it, may be impossible.

These issues raise two fundamental sets of questions. The more difficult of the two is: why should elephants be controlled, while the second is how such control should be conducted?

"Playing God" is the frequent criticism (Sheldrick 1993) - including by an anonymous reviewer of the original paper - of wildlife managers who intervene in the natural course of things. In this sense, the elephant problem in KNP is self-imposed, but the decision to control elephants is based on the acceptance of the responsibility of not allowing the consequences of an uncontrolled increase in the elephant population (Joubert 1986; Whyte *et al.* 1999). The obvious experiment of letting the elephants increase could have unfortunate consequences to the ecosystem and the other species that are dependent upon it. Such "experiments" elsewhere in Africa have demonstrated some of the consequences for biodiversity (Cumming *et al.* 1997; Herremans 1995; Leuthold 1996; Western & Gichohi 1989).

These consequences raise more questions. Did elephants effect such ecosystem changes in the past? If so, should they be allowed do so now? What processes regulated elephant numbers in the past? And what is 'natural' today in an Africa with a large and rapidly growing human population and few well-protected parks?

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Given the choice of controlling elephant numbers, does KNP's management have effective alternatives to killing elephants? The use of contraceptives has been considered a promising solution (Short, 1992; The Economist, 1996). Consequently, much effort has been spent investigating the endocrinology of elephants and to evaluate the potential use of substances such as RU 3486 that may block implantation (Greyling *et al.* 1997; Greyling *et al.* 1998). Other methods based on either immunocontraception or slow-releasing oestrogen implants have received research attention in KNP (Fayrer-Hosken *et al.* 2000; Part 2 of this chapter).

Some of the potentially serious and unpredictable consequences to the individuals of these methods are discussed later in this chapter. These include changes in behaviour, social status within the breeding herd, possible changes to the structure of social units and the population itself (Whyte In Press), and in the steriogenic activities of the ovary and uterus. Cows treated with oestrogen implants may remain in an extended state of oestrus (Whyte *et al.* 1998). The prediction of the effects that these may have on their behaviour, or the consequences that this may have for the Park's male elephants is not possible (Whyte *et al.* 1998).

Finally, the question is asked: what is the smallest number of animals one could kill or sterilize if the goal is to control population growth? The answer to this identifies the age and sex group where natural processes (mortality or survival rates) would make the largest difference to whether the elephant population increased or decreased.

Why control elephant numbers?

In some dry forests, increasing numbers of elephants have progressively converted woodlands into more open habitats (Laws, 1970; Barnes, 1980, 1983; Douglas-Hamilton, 1987; Dublin, 1995; Dublin *et al.* 1990; Jachmann & Croes, 1991; Leuthold, 1996; see Lawton & Gough 1970, Guy 1982 and Ben-Shahar 1996 for alternative explanations). By comparing ecosystems on either side of an elephant fence in Miombo woodlands, Cumming *et al.* (1997) demonstrated significant reductions in the species richness of birds, ants and other taxa, where elephants have removed the tree canopy. In KNP, elephants also suppress the rejuvenation of selected woodland trees (Viljoen 1988; Trollope *et al.* 1998).

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There are several reasons why the prevention of these changes are desirable. Biodiversity considerations have been used to justify the maintenance of low elephant numbers (Joubert 86). On the African continent where so little protected habitat remains, there may be the need to conserve a set of species more localized and thus more vulnerable to extinction than elephants (Hoeft & Hoeft 1995). This justification explicitly recognizes that restoring nature to its original state or states on the original scale is now impossible.

Alternatively, the target size that the population must not exceed may be historically justified. It is reasonably sure that elephant densities in KNP are now different from the recent past (see Chapters 3 and 4). Evidence suggests that KNP held only low numbers of elephants at the turn of the century (Bryden 1903; Stevenson-Hamilton 1903a; Vaughn Kirby 1896). Whether these were naturally low numbers or, as Spinage (1973) has argued, the consequences of the ivory trade, will continue to be debatable.

If the latter explanation is correct, then elephants should naturally have been abundant which raises the question: why there were any areas originally with extensive woodlands? Elephants might increase over century long time scales, destroying the woodlands in the process, and thus causing their own decline (Caughley 1976). Elephants and woodlands could therefore only have co-existed over very large temporal and spatial scales that permitted large mosaics of woodland habitats in various stages of elephant-induced decline or recovery. Finely resolved palynological data might elucidate such changes, but no references to such studies over sufficiently large areas could be located.

In current times, where most national parks and reserves constitute islands in man-modified landscapes, even KNP's 20 000 km^2 may be too small to allow such cycles to operate. The idea of trans-frontier conservation areas (TFCAs) - huge protected areas that stretch across international barriers - may ameliorate some problems of geographic scale, but the realization of such parks in elephant range is still in the future (Braack 2000).

If the explanation that elephants were always at low numbers is correct, then what were the

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probable reasons for this and what has changed? The answers lie in elephant demography – a high pre-breeding mortality rate in cows could limit a population.

MATERIALS AND METHODS

Parameters

A simple spreadsheet model was constructed to explore the options for contraception and other forms of management in the KNP elephant population. Demographic parameters for the model came from data collected at routine culling operations in KNP. All elephant culled during the years 1976, 1977, 1978, 1979, 1987, 1988, 1989, 1990, 1991, 1992, 1993, 1994 and 1995 were examined (n= 4 739).

Relevant data collected from all culled animals were age (after the method of Laws 1966), sex, reproductive status of cows (pregnancy, lactation), and foetal mass and sex.

Inter-calving period was calculated from the period of anoestrus using the formula (after Hanks 1972):

$$X\ (\textit{Period of anoestrus}) = \frac{\textit{Gestation time} * \textit{No. adult cows non-pregnant}}{\textit{No. adult cows pregnant}}$$

Mean calving interval (MCI) = Period of anoestrus + gestation time.

Population growth and mortality rates used in the model

Annual mortality was estimated from the numbers culled and population growth despite it. Only two factors can contribute to population growth – births and immigration from areas outside the KNP. Between 1976 and 1994, KNP was fenced in its entirety (see Chapter 5), and thus immigration would have been negligible.

Between 1973 to 1994 inclusive, the population was stabilised through culling as it ended this period at much the same size (7 800) as it started (7 600), but showed some fluctuation in between. During this time the population always increased when the cull was less than 5%, making this (5%) a reasonable estimate of the population's growth rate. Given the estimated parameters of age at first parturition and subsequent inter-calving period, the

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model was used to calculate mortality through the difference between the potential growth rate and the actual population growth of 5% as estimated above.

The spreadsheet model

The model (Whyte *et al.*1998) assumes constant survivorship up to 60 years (and no survivors beyond that age), and specifies the age of first calving, and calving interval. In nature, these parameters are not independent: poor food conditions and high elephant densities will probably affect all three (see van Aarde *et al.* 1999). In particular, Dobson (1993) summarizes data showing how the age at first calving declines with increasing elephant densities. The effect of density on inter-calving period is less obvious. The model assumed no marked changes in numbers - for that is the management objective - and so, for simplicity, each parameter was fixed at a given value.

The foetal sex ratio for elephants in KNP is 1:1 - culls yielded a sample of 311 male to 313 female foetuses. This concurred with the findings of Smuts (1975). This ratio persists until 14 years old, when the young males leave the breeding herds and join bachelor groups. The mortality of bulls in bachelor groups is unknown. It is likely to be slightly higher than in adult cows, but still low, as KNP has recorded few natural deaths of adult bulls. In the model, it was assumed only that there were sufficient males in the population to permit the cows to produce young whenever they were able to do so.

Growth rates under the combinations of maximum and minimum values of the three reproductive parameters discussed so far were explored (survivorship up to 60 years, the age of first calving, and calving interval). The objective was to find the parameter in which change would have the greatest effect on KNP's elephant numbers.

RESULTS AND DISCUSSION

Elephant demography

It takes only a simple demographic model to show that elephants can increase rapidly in numbers. Female elephants have a life span of ~60 years, with between 2.5 and 5% of the population dying each year (Laws & Parker 1968; Laws *et al.* 1975; Jachmann 1980;

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Dunham 1988 and references therein) have summarized these and other demographic parameters. They have a mean age of first calving from 11 to 20 years old. Gestation is 22 months (Kenneth & Ritchie 1953; Lang 1967), and the inter-calving interval can be as short as three years or as infrequent as nine years. They remain fertile into their late fifties.

In KNP, some cows have given birth in their 12th year and most have given birth by the time they are 13 years old (Smuts 1975; see Chapter 4). A culled sample of 966 adult cows shows an almost exact equality in the numbers of those pregnant (484) and non-pregnant (482). This means that, on average, a cow is pregnant for half of her adult life. Thus the calving interval will be twice the gestation time of 22 months. After the method of Hanks (1972), the inter-calving period was estimated at 43.9 months or 3.65 years.

There is no long-term, cohort-based study of survivorship so annual mortality was estimated from the size of the cull itself and how fast the numbers grew despite it. Only two factors can contribute to an increase in the population: births and immigration from areas outside the park. Immigration from Mozambique was probably a major cause of increase prior to 1976. It is less likely to explain the changes in the last two decades due to the fencing of KNP (Walker et al., 1987; see Chapter 4). There were few elephants in the conservation and agricultural areas to the west, and KNP was fenced along northern and southern boundaries in 1970 and on the eastern boundary by 1976. Immigration could only have made a small contribution to the population's growth rate after 1972, but whatever its contribution, it was included in the calculations as if it were a birth rate.

From 1973 to 1994 inclusive, the cull averaged 6.7% of KNP's elephants. The population ended this period at much the same size (7 800) as it started (7 600) and numbers fluctuated between a low of 6 900 and a high of 8 700 animals. From year to year, the population always increased when the cull was less than 5%. It increased from one year to the next in nine different years when the cull was 0, 4, 4, 4, 4, 5, 5, 5 and 6% of the population respectively. Given the inevitable uncertainties in counting animals, increases may reflect under-counting in one year followed by over-counting, in the following year. The single high value of 6% was discounted because of this possibility. The consistent increases in

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population when between 4 and 5% of the animals are killed thus makes 5% a reasonable estimate of the population's growth rate. Using the parameters of each cow calving for the first time in their 12th year and at 3.6 years thereafter, the model estimated population growth at 6.5%. The difference between this and the estimated 5% growth rate, allows the calculation of annual mortality rate at 1.5%. These parameters differ from those calculated at a later time (see Chapter 5, Part 2)

If these rapidly growing elephant populations are not typical of KNP's original state, then what has changed?

With this model, the elephant population can increase when mortality rate is as high as 5% per year and when age at first calving is as late as 20 years. In contrast, when the inter-calving interval is as long as nine years, the population can only grow slowly under the best circumstances of low mortality and early age at first breeding. Given the natural range of parameters, the inter-calving period played the major role in driving the population changes. This conclusion is similar to that of Dobson (1993) and Hanks & McIntosh (1973).

Changes in the calving interval are probably the main reason for the numbers of elephants now being higher than in the past. This difference in numbers may also be the result of short calving intervals combined with high pre-breeding mortality (which is demographically equivalent to long calving intervals). The interval between a cow producing a youngster of breeding age is long in both circumstances. Various factors could have influenced this parameter.

Juvenile (i.e. pre-breeding) mortality might have been consistently higher in the past. Hunting by Stone- or Iron-age cultures might have been responsible. So, too, might the long distances between water sources - for young elephants are prone to die during droughts (Dunham 1988). More recently, KNP's extensive network of artificial water holes may have positively influenced pre-breeding survival as the droughts in the early 1980's and 1990's had little effect on the growth rate of KNP's elephants, though Walker *et al.* (1987) reported elephants doing unusual amounts of damage to trees at the time.

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The demographic model suggests that juvenile mortality caused by droughts could be episodic and still slow growth rates to near zero. One episode in every 11 years would be enough to severely impact all the pre-breeding age classes.

The parameters for KNP's elephants (age at first calving, inter-calving interval, and annual survival) are close to, or exceed the maximum observed elsewhere. Calef (1988) suggests 8% as the theoretical maximum growth rate for elephants. Age-structured models similar to those of Dobson (1993) were employed and the results produced by the model agree with Dobson that this seems to be too high. KNP's particular problem is to regulate elephants at a density at which resource limitation is minimal. The management problem is how to achieve this. Broadly, there are only three options – contraception, translocation, culling or a combination of these. The model allows some insights into contraception and culling options.

Contraceptive options for managing elephants

Contraceptives allow the extension of the inter-calving interval and so offer a potentially effective way of controlling population numbers. Using the demographic model introduced above, the proportion of KNP's roughly 3 000 reproductively active female elephants that would require contraceptive treatment was calculated. To ensure zero population growth, the average calving interval would have to be reduced to about 12 years, or about 75% of all cows >12 years (n = about 2 250) would have to be under treatment. Furthermore, a zero population growth rate will only be attained after 11 years of treatment because in that 11-year interval, females born before the use of the contraceptives are steadily recruited into the breeding population. Indeed, 11-year-olds are the largest breeding class, since there cannot be more 12-year-olds than 11-year-olds, 13-year-olds than 12-year-olds, and so on. Consequently, the breeding population increases at about 4% per year to over 5 000 adult cows before zero population growth is attained. Thus, the final effort would require ≅4 000 animals to be under treatment - not the initial number of 2 250 (75% of 3 000).

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The parameter for which there is the least confidence is annual survival. It is a back calculation that assumes a particular growth model and further assumes how the population would have grown without the cull. If the annual mortality rate is increased from the 1.5% employed in the previous paragraph to 2.5%, then the required fraction of cows treated with contraceptives declines only from 75% to 61%. Simply, it is the very short inter-calving interval of KNP's elephants that compounds the management problem.

The model also confirms Dobson's result that using contraceptives to delay the age at first calving, is an even less effective strategy than changing the inter-calving interval.

Consequences of contraception for the individual

Contraceptive use aims to control the elephant population without the killing of animals that some people find objectionable (Landman 1978; Sheldrick 1993). It also holds the desirable promise of being reversible. Were some natural event to greatly reduce the population, the contraceptive programme could be stopped and the population could recover quickly. In spite of limited information, some of the physiological and behavioural consequences of the substances presently on trial as contraceptives may be predicted. These consequences may thwart the promise of contraception as both humane and reversible (see Part 2 of this chapter).

Studies on endocrine correlates of elephant reproduction show that blood levels of both oestrogens and progestins are relatively low in the African elephant (Plotka *et al,* 1975; de Villiers *et al.* 1989). In contrast to most other mammals, relatively high concentrations of the 5-reduced metabolites of progesterone (rather than progesterone itself) appear to maintain pregnancy in the elephant (Hodges *et al.* 1994; Hodges *et al.* 1997; Greyling *et al.* 1997), but as yet, the role of progesterone in the maintenance of pregnancy can not be discounted. Elephants may be extremely sensitive to this steroid, resulting in extremely low concentrations being sufficient to support pregnancy. This may also be true for the interactions between oestrogens and ovarian function.

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Circulating concentrations of oestradiol-17 are extremely low (Plotka *et al.* 1975; McNeilly *et al.* 1983) and endometrial receptor affinity is highly specific (Greyling *et al.* 1997; Greyling *et al.* 1998). Oestrogens in the elephant, as in other mammals, probably originate from developing ovarian follicles. Ovulation and incidences of oestrus may be associated with a surge in their plasma concentrations but circulating levels are extremely low (Hess *et al.* 1983).

Slow-releasing capsules implanted in ten lactating elephants in KNP apparently resulted in continued high concentrations of oestradiol-17. The consequences may have been an impairment of lactation and a subsequent increase in calf mortality (Whyte & Grobler 1998). Moreover, the treated cows remained in a continuous state of sexual heat. They appeared to have been continuously harassed by bulls (Whyte & Grobler 1998; see Part 2 of this chapter) which resulted in separation from their breeding groups and even their calves. This may also have contributed to the reduction in calf survival.

Considering the influence of sexually associated aggression in bulls on calves, the high incidence of cows in heat, may also have major consequences for the unsuspecting tourist. At any given time at least some 2000 cows will be experiencing this condition should oestradiol contraception be employed (see below). In addition, the potential for continued high levels of oestrogens to induce the carcinomic growths that have developed in other species (Li *et al.* 1983; Li *et al.*, 1988) can not be discounted.

Results of recent research in immunizing elephant cows with porcine zona pellucida antibody (pZP) in KNP suggest that animals will have to be given an initial vaccination and two subsequent two-weekly boosters to raise antibody titres to effective levels, and at yearly intervals thereafter to ensure contraceptive effectiveness (Fayrer-Hosken *et al.* 2000). Immunocontraception is effective in several free-ranging mammal species (Miller *et al.* 1998 and references quoted therein). The method's protagonists (see Bertschinger et *al.*, 1996) claim minimal effects and even reversibility (Kirkpatrick *et al.* 1992; Kirkpatrick *et al.* 1996; Fayrer-Hosken *et al.* 2000; Turner *et al.* 1992). Others claim evidence to the contrary in some species (see Mahi-Brown *et al.* 1989; Paterson *et al.* 1992; Paterson *et al.*

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1996). Active immunization with the zona glycoprotein induces infertility. It also causes ovarian dysfunction and ovarian pathology characterized by a lack of folliculogenesis and depletion of the primordial follicle population (Paterson *et al.* 1996). If this proves to be the case for elephants, such sterilized individuals would be removed permanently from the gene pool - an effect similar to that achieved through culling. However, ongoing research in KNP has now suggested reversibility in at least some of the previous research animals (Fayrer-Hosken *et al.* 2000).

In summary, all of the methods currently under test have serious known or predicted possible consequences to the health of the cows, their behaviour, and those animals around them. This is not the only problem with contraceptives.

The necessity of boostering antibody titres through repeated injection means that all animals under treatment must be treated according to a schedule. In order to achieve this, it would be necessary to locate the animal as and when its booster was due. The only way to do this would be to fit the animal with a radio collar. The logistics and expense of this for 4 000 elephant cows would be prohibitive. From a tourism point of view, 4 000 elephant cows with radio collars would be unacceptable.

Other management options

Another option is translocation or the removal of live animals from the KNP to other reserves elsewhere. In its effect on the population, it is the same as culling as individuals are permanently removed from the gene pool. Like contraception, translocation would be favoured as it is a non-lethal option. But while KNP has developed its capacity to move entire family units and even the largest of adult bulls, the markets for such animals are extremely limited. Current demand is in the order of 60 animals a year which could not serve as an alternative to larger scale methods. However, the establishment of the proposed large TFCA in the Coutada 16 area of Mozambique (which borders on KNP's eastern boundary) would offer considerable translocation options in future (Braack 2000).

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The model offered a numerically simpler solution to the KNP's elephant management problems. Rather than kill hundreds (even thousands) of elephants each year, or contracept several thousand cows, the killing of a much smaller number of cow elephants just prior to their first pregnancy would achieve the same aim. The culling of a mere 300 carefully selected animals each year would drive the population to extinction, for no breeding cows would enter the population. Culling 250 would stabilize the population.

The words 'sterilize' or 'translocate' can be substituted for 'cull' in the previous paragraph and its conclusions would be unchanged. Translocation of juveniles is not possible, as live removal of juveniles not in family units has been specifically precluded as a management option (Whyte *et al.* 1998; 1999).

Contraception and sterilization are not usually considered synonymous. Indeed, the efforts discussed above aim to find reversible contraceptives and to avoid sterilization, but for some individual research animals this might be the unintended consequence of our ignorance of how the contraceptives function. If sterilization, and not contraception, is to be an *intended* objective, then it should be stated as such. The ethical issues this raises will then have to be scrutinised and the research programme focused on deliberate sterilization.

CONCLUSIONS

There are four options for the management of KNP's elephant population. Since 1967 the choice was to cull excess elephants to maintain the population at around 7 000 (up to 1 850 in a year) to protect against loss of biodiversity. The other three options are to let elephants increase (with probable negative consequences for biodiversity), to cull or sterilize 250 pre-breeding cows, or to administer contraceptives to 75% of all breeding cows.

There is nothing sacrosanct about keeping the elephant population at its current level. There could be a choice of any combination of the four options, including higher elephant numbers, likely higher inter-calving intervals and so a proportionately smaller number of animals culled, contracepted or sterilized, but with more damage to the woodlands. The optimal balance between elephant numbers and woodland is not easy to determine without

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long-term, large-scale experimentation. Moreover, with larger numbers of elephants, the absolute numbers to be killed, contracepted or sterilized would also be larger.

There is still a debate about whether or not woodland - and the low elephant numbers that permit its existence - was naturally the permanent or even an episodic state of this region. What is certainly not natural is the small fraction of protected land in Africa (and elsewhere), the consequent rates of global extinction, and the loss of ecological processes across the landscape. Protecting woodland may be essential to preserve a representative sample of species and processes for the future, whatever the past may have been.

If there were few elephants in the past, then the first question is why? The second is how do we keep elephant numbers low? The numerical targets required for zero growth range from selectively killing or sterilizing a few hundred 11-year-old cows to indiscriminately culling many hundreds of animals, to using contraceptives on several thousand adult cows. There will also be some individuals who find killing, any elephants an anathema. Unfortunately, the use of contraceptives on this scale is completely impractical and they are likely to have severe behavioural, physiological and demographic side effects. Should elephants be unnaturally culled or sterilized prior to calving for the first time, or be left to die naturally of thirst or starvation in dry years? This is an ethical issue that scientists are not solely equipped to judge. Such a decision should be a collective value judgement distilled from the public at large.

Identifying the smallest numerical target for controlling elephant numbers is not just a practical convenience. It is the most likely target for how the vagaries of nature limit elephant numbers. The high mortality of juvenile elephants may explain why some populations have remained at numbers that do not lead to the destruction of woodlands. In this sense, the smallest target for control is also likely to be the most natural one. Whatever the ethical issues of sterilizing female elephants, it does provide the smallest numerical target and it avoids killing animals.

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CHAPTER 6: PART 2:
ELEPHANT CONTRACEPTION RESEARCH IN KRUGER NATIONAL PARK

INTRODUCTION

Part 2 of this chapter was compiled from a paper examining the status of research into elephant contraception in KNP (Whyte & Grobler 1998). Two contraception techniques received research attention in the KNP over the past 4 years. The first of these was the "immunocontraception" method conducted jointly by the Science and Conservation Biology Program, Montana, the Faculty of Veterinary Sciences at the University of Pretoria and the Humane Society of the USA. Immunocontraception uses porcine zona pellucida immuno-contraceptive vaccine (pZP) to stimulate the target animal's immune system to prevent sperm penetration of the ovum (Kirkpatrick *et al.* 1992; 1996).

The other technique used hormonal control through the surgical subcutaneous insertion of oestradiol-17ß implants and was conducted by the Institute for Zoo and Wildlife Research, Berlin.

Both of these projects had certain potential problems associated with them which were either addressed in the project protocols or were expressed by members of SANP's Department of Scientific Services (DSS) at the time the projects were initiated. These were social disruption, threats to the health and welfare of the treated animals and/or their calves, and behavioural aberrations. It was the intention of the paper (Whyte & Grobler 1998, and this part of this chapter) to put the findings of the research groups into a management perspective, and to report on the behavioural data collected by SANP staff.

Management concerns

Immunocontraception

i. Possible permanent damage to the cows' ovaries resulting in sterility (see Mahi-Brown *et al.* 1989; Paterson *et al.* 1992; Paterson *et al.* 1996).

ii. During courtship in elephants, oestrous cows can be extensively chased by bulls (Moss 1988). If the cow is not ready to mate, she will try to prevent him from

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mounting by running away. The chasing continues until she does become receptive. This causes a certain amount of disturbance to other members of the family unit. Normally copulation and conception would result, and this disturbance would not be repeated until her next oestrous period after her calf was born (3.8 – 4 years). Under pZP treatment, the cow would mate normally but would not conceive, and would then "cycle" and return to oestrus in about 15 weeks (Kapustin *et al.* 1996; Plotka *et al.* 1988). The frequency of mating and its accompanying disturbances would be far more frequent.

Oestradiol-17ß implants

i. Oestrogen is a known carcinogenic in some species (Li *et al.* 1983; Li *et al.* 1988) when used in the dosages required to prevent conceptions. No information is available on the potential effects on elephants.

ii. Oestrogen is an agent which may induce abortions. Abortion of a near full-term foetus could have serious consequences for an elephant cow. The research group used an ultrasonic scanner to determine reproductive status of the proposed research animals prior to insertion of implants. Only adult cows which had recently calved would be non-pregnant, and all ten of the cows selected as study animals had very young calves at foot. In spite of this, there was some concern as to whether the scanner would be a reliable indicator of pregnancy, and that there thus existed a possibility of mistakenly treating pregnant cows with oestradiol.

iii. As the treated cows would pass the metabolised oestradiol out through their urine, it was suspected that this might incorrectly signal to bulls that they were sexually receptive. Cows in this condition could be continually chased or harassed by the bulls, and this could last for as long as the implants remained active. This would be stressful for the cows and even more so for their calves. Calves of less than a year old are very seldom to be found more than a few metres from their mothers (Moss 1988). If these cows were continually harassed by attendant bulls, the calves would be in danger of:

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- Being trampled by bulls (or by the mothers themselves in their efforts to avoid the bulls).
- Being unable to suckle adequately as a result of the disturbance, possibly resulting in malnutrition and death from starvation.

iv. High levels of oestrogen are known to have a suppressive effect on milk production in some species (Lammers *et al.* 1999). If this occurs in elephants this may also lead to malnutrition and possible death of the calves.

v. High levels of oestradiol may cause permanent damage to the ovaries and thus permanent sterility.

vi. High levels of oestrogen in horse females is known to induce diarrhoea in foals through ingestion through the milk - another possible health risk to elephant calves.

vii. Concerns were expressed over the possible effects that elephant cows in false oestrus may have on bulls and on their behaviour such as heightened aggression (Whyte *et al.* 1998; Scott, In litt.[1]).

METHODS & MATERIALS

Immunocontraception

A sample of 21 non-pregnant adult cows was immobilised and fitted with radio-collars to facilitate relocation and identification of each animal. Each was given an initial inoculation of pZP vaccine at the time of immobilisation. Treated animals were remotely given a "booster" inoculation six weeks later. This was delivered remotely by darts fired from a capture gun from a helicopter into the rump area of target animals. A second booster was administered six months later, and thereafter cows were immobilised at six-monthly intervals for ultrasonic examination of their reproductive status (Fayrer-Hosken *et al.* 2000).

[1] Mr P. Scott, Senior Ranger, Kruger National Park.

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Two of the collars malfunctioned leaving a research sample of 19 animals. Another 21 cows were immobilised and radio-collared to serve as controls.

Due to a high proportion of these cows conceiving after treatment, a second group of ten research cows were treated under a revised vaccination schedule (Fayrer-Hosken *et al.* 2000). Behaviour of these animals was not monitored. Results of this research receive some attention under "Discussion".

Oestradiol-17ß implants

A second sample of 10 adult cows was immobilised and fitted with radio-collars to facilitate relocation and identification of each animal. As with the pZP treated cows, they were selected by having a small calf at foot. These cows each received five slow-release oestradiol-17ß "negative feedback" implants, inserted sub-cutaneously behind the ear in the neck area (Meyer *et al.* Undated).

After six months, when oestrogen levels were expected to decline, these cows were supposed to receive a second implant. This second phase was not implemented and the project was suspended due to behavioural aberrancies which were induced by the high levels of oestrogen. These cows were also subsequently examined at six-monthly intervals for ultrasonic examination of their reproductive organs. These results also receive brief attention in the discussion.

Behaviour

No provision was made for behavioral monitoring in either of the projects' research protocols, but SANP were alerted to the possibility of adverse behavioural and other negative side effects of the oestradiol implants (van Aarde In litt.). Monitoring was instituted in haste after the animals had already received their initial treatments. It was not initially expected that the immunocontraception vaccine would have any significant adverse effects on behaviour, but once the monitoring program had been instituted for the oestradiol implanted animals, the behaviour of pZP treated animals was also monitored.

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Behavioural monitoring had not been foreseen during the planning phase, and most of the research animals were selected close to Skukuza (the administrative centre for KNP) for logistical convenience. Unfortunately this proved to be in areas largely unsuitable for this monitoring due to thick bush and mountainous terrain, which complicated data collection. Research animals could not always be observed due to the danger of approaching them on foot in the thick bush.

A flaw in the methodology identified later was that behaviour of the control groups was not also monitored. As it had been assumed that the pZP-treated animals' behaviour would not be affected, data was only collected for comparison of the animals treated with pZP and oestradiol respectively. Data collection focused on the presence (or not) of bulls and any behaviour directed at treated cows, and survival of calves.

Treated animals were tracked regularly from the ground for a six-month period after treatment for attempted data collection. Aerial tracking from a Cessna 182 was also occasionally also used when ground tracking had been unsuccessful.

Data on calf survival and condition of the cows' reproductive organs were collected by the contraception researchers when their animals were subsequently immobilised for ultrasound examination.

RESULTS

Only the results of the behavioural monitoring are discussed here. Results of the contraception research receive some attention later in the chapter, as they are relevant to the conservation management of KNP's elephants.

Behaviour

Immunocontraception

Research animals could only be observed on 23 (40.4%) of the 57 times these animals were tracked from the ground. In 56 of the 57 attempts (98.2%), it could be determined that the cow was with the herd (had not been separated from the herd). Their calves were recorded

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with them on all of the 23 occasions when the treated cows were seen. Bulls were recorded with the herds only nine times (15.8% of the 57 tracking attempts).

No behavioural abberancies such as harassment or attempted matings by bulls were recorded from the pZP treated animals.

Oestradiol-17β implants

On 112 of the 122 tracking attempts (91.8%), it could be determined that the cow was with the herd, but due to the nature of the terrain, the target animals were seen on only 67 (59.4%) of these occasions. Their calves were seen with them 60 times (89.6%). Bulls were recorded with the herds on all of these tracking attempts, and harassment of cows by these bulls was observed 15 times of the 67 occasions (22.4%) that the cows were seen.

Evidence for harassment of cows by bulls was obtained on video tapes by the students conducting the observations. Recordings were made of bulls with penis erect following the treated cows, and of red mud smears on a cows back which were clearly from the front feet of bulls trying to mate with her.

There were clear differences between the data collected from the two groups of research animals, particularly with respect to the relative number of times that calves were absent from their treated mothers, the number of times that bulls were recorded in attendance with these cows, and the number of times that "harassment" was recorded (Table 15).

Calf mortality

Six months after the insertion of the Oestradiol implants, one of the 10 calves had disappeared. This project was terminated at this point, but ultrasound examination of the treated animals continued at six-monthly intervals for a further three years, when the collars were removed. At this time another two of the calves were no longer with their mothers. This was significantly different to the pZP treated cows who had lost none of their cows after the same period ($\chi 2 = 7.94$; $p < 0.005$).

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Table 15: A statistical comparison of behavioural parameters recorded for free ranging African elephant cows exposed to two different contraceptive treatments.

Variable	Treatment				Chi-square value	p
	pZP vaccinations		Oestradiol-17 implants			
	Yes	No	Yes	No		
Treated cow noted within herd	56	1	112	10	4.02	<0.05
Calf noted present with cow	23	0	60	7	4.27	<0.05
Bulls present in the herd	9	14	67	0	43.77	<0.001
Bull harassing the treated cow	0	23	15	52	4.67	<0.05

Aggression by bulls

A report was received from Scott (In litt.) expressing concern over an increased incidence of aggression by elephant bulls towards tourists in the Boesman Wilderness Trails Area subsequent to the commencement of this research. This he attributed to an increase in the number of "musth" bulls attracted to the area utilised by oestradiol treated cows.

DISCUSSION

Immunocontraception

The results of the tracking of the cows vaccinated with pZP were as would have been expected from cows whose behavioural patterns were not affected by the treatment. The calves were always with their mothers and, although bulls were occasionally recorded with these herds, this is normal as bulls do enter the herds to investigate the possibility of cows being in oestrus or for other social reasons (Moss 1988).

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The efficacy of this method was initially somewhat under question, as after 12 months, nine of the 19 cows were pregnant. This was attributed to the vaccination schedule with long inter-booster periods which resulted in these cows conceiving before antibody titres had achieved levels high enough to prevent conception.

The second project used a revised vaccination schedule which was significantly more effective as only two of the ten treated cows conceived (Fayrer-Hosken *et al.*2000).

This treatment has also shown that it is reversible and that vaccination of a pregnant cow has no effect on gestation, the foetus or parturition (Fayrer-Hosken *et al.*2000).

Oestradiol-17ß implants

The cows treated with the slow-release oestradiol-17ß implants showed definite behavioural differences to those treated with pZP. Cows became completely separated from their matriarchal groups on 10 of the 122 occasions that they were tracked. On one occasion, the cow was tracked by fixed wing aircraft and was found on her own in the company of seven bulls with no other cows or calves anywhere nearby. Bulls were recorded with the herds in a far greater proportion of times, and harassment of the cows was recorded in about 25% of all observations. Bulls were recorded trying to mate with cows during darting and video material also showed overt courtship behaviour. Cows do become separated from matriarchal groups during courtship and mating (Moss 1988), but this lasts only for a few days during which time the cow is receptive and willing to mate, and the calf is old enough to be separated from its mother for short periods. With the oestrodiol treated animals, the "false" sexual heat appears to last for the full duration of the treatment. The cows were not receptive and willing to mate, and under these conditions, the attentions of the bulls must be considered to be harassment, particularly with the added stress of being separated from their young calves.

Separation of small calves from their mothers is highly unusual (Moss 1988). One of the ten calves disappeared within six months and two more within three years. Although this could

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not be directly attributed to the oestradiol treatment, the results suggest that this was likely as none of the pZP treated animals' calves disappeared.

Elephant cows appear to be highly sensitive to oestradiol. At the dosage rates used, ultrasonic scans showed that after three years, all of the 10 cows showed no sign of ovarian activity and that the treatment had probably caused permanent sterility (D.G. Grobler personal observations).

CONCLUSIONS

It is the stated objective of SANP to reduce numbers of elephants in the designated "Low-impact Zones" and to stabilise them in the "Botanical Reserves" (Whyte *et al.* 1999; see Chapter 7). Various methods of achieving this are at the disposal of KNP managers (Whyte *et al.* 1998), but the ultimate objective is to do this by non-lethal means. Only two methods comply with this objective – translocation and contraception. Whyte (In press) examined the advantages and disadvantages of these two methods, and neither are likely to offer any long-term solution.

Translocations are expensive , markets are limited and ultimately, areas receiving translocated KNP elephants will be faced with the same biodiversity concerns. The proposed TFCA in the Coutada 16 area of Mozambique (Braack 2000) may offer a considerable opportunity to dispose of excess KNP elephants through translocations, but once this area has been stocked, further translocations out of KNP seem very unlikely.

Contraception is clearly not yet at the technological level where it would be usable as a management tool for large populations in large conservation areas, but the pZP method shows considerable promise for small populations such as have arisen recently in many parts of South Africa through translocations. The method needs further research to determine the reasons for some of the cows conceiving while under treatment.

This study could show no evidence to suggest that the immunocontraception technique had any adverse effects on the behaviour of either the treated cows, their matriarchal groups or

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the bulls. Other management concerns such as the possibility of causing permanent sterility and the long-term effects of cows not conceiving and continuously returning to breeding condition will require some attention. Also the impacts of contraception on matriarchal group size may raise some other ethical concerns.

The physiological and behavioural side effects experienced by the oestradiol treated cows are be considered unacceptable as they must have placed severe stress on the treated cows and their calves, and the project was terminated on both humane and ethical grounds. It would also seem that the oestradiol has caused permanent damage to the ovaries of treated cows, which in itself is likely to render the method unusable as reversibility is a requirement. A population stabilised through sterilisation of the majority of breeding females would be at risk from disease as an epidemic would be less capable of recovery without a breeding nucleus.

Finally, the implications of sterilising young females of a species with a highly developed sense of family and depriving of the opportunity of participating fully in their matriarchal groups should deserve sincere ethical consideration.

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CHAPTER 7: THE NEW POLICY FOR THE MANAGEMENT OF THE ELEPHANT POPULATION OF THE KRUGER NATIONAL PARK

INTRODUCTION

This chapter was compiled from the SANP's new elephant management policy for the KNP (Whyte *et al.* 1997) which was also published (Whyte *et al.* 1999) to achieve a wider dissemination.

The policy of culling elephant as part of the management strategy of the KNP has always been somewhat controversial. In late 1994 the issue was again debated when the reasons for culling and the ethical morality of killing elephants were raised by certain animal rights groups. This resulted in a public debate being held in Midrand on 4 May 1995, at which SANP undertook to review its policy for the management of elephant in the KNP. In accordance with this undertaking, a series of meetings and workshops were held in order to reconsider the policy and make recommendations on appropriate management for the future. The policy is the product of many hours of consultative debate between SANP and a wide diversity of interested and affected people and organisations.

The first of the workshops directed at developing a management policy was held in Skukuza on 8 February 1996 in conjunction with members of the African Elephant Specialist Group (AfESG). This was followed by a meeting two days later with delegates of the AfESG and the International Fund for Animal Welfare (IFAW). The new rationale was summarised in a document prepared by Hall-Martin & Novellie (1996).

On 30 October 1996 at a workshop held in Skukuza, a wide-ranging series of possible management options were listed and debated. The results of this meeting were reported by Whyte & Biggs (1997). The options debated were:

i. The previous management policy was correct.
ii. There are too many elephants.
iii. There are too few elephants.
iv. The KNP ecosystem needs natural fluctuations of elephants.
v. The KNP ecosystem needs controlled fluctuations of elephants.

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vi. "Animal rights" *(Laissez-faire)* type of policy (no culling).

vii. Community involvement/sustainable consumptive utilisation.

viii. Maximising economic opportunities.

The resolutions accepted by this meeting were that:

i. The National Parks Board mandate and primary responsibility within the KNP was to conserve *all* elements of biodiversity and not to manage selectively for the benefit of a single species such as elephant. Although elephants are considered important (even essential) ecosystem components, they are not *more* important than any other component.

ii. Wildlife populations do not remain static through time and space, and consequently elephants should not be maintained at a stable unvarying population ceiling, but rather that fluctuation in numbers and density should be introduced to simulate ecosystem processes and enhance biodiversity.

iii. In contrast with all other known animal species, elephant (and possibly rhino) do not respond to short-term climatic cycles. It was recognised that unimpeded population growth would have negative impacts on other wildlife in an unnaturally limited "conservation island", and therefore some form of population control would be necessary for elephant (and perhaps eventually rhino).

iv. There is evidence of severe impact by elephant at current densities in certain areas of the KNP so that such areas may already have reached threshold levels of elephant density.

The implication therefore was that Option ii above (there are too many elephants) would be how the elephant population management issue should be approached in future. There was consensus that the consequences of unrestricted elephant population growth resulting in an ultimate self-induced population crash are not acceptable.

These resolutions were presented to the public during the debate held at Midrand on 12 November 1996. Very little comment was voiced by the meeting's participants, either to these

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resolutions or the Hall-Martin & Novellie (1996) document, which was then accepted by the SANP as a mandate to proceed with defining the detail of this new policy proposal.

The first step in doing this was the convening of a workshop to discuss the maintenance of biodiversity in the KNP. A wide variety of scientific expertise, both national and international, was invited to participate in this workshop which was held between 11-13 February 1997. As it was accepted that an increasing elephant population was likely to have some negative consequences for KNP's biodiversity, the focus of the workshop was to establish "Limits of Acceptable Change" (LACs) in a wide spectrum of environmental variables. However, the concept of acceptable limits of change was soon rejected as it was felt that in many instances, the knowledge or understanding of the system was simply not adequate to know how much elephant induced change could be regarded as "acceptable". LACs were redefined as "Thresholds of Potential Concern" (TPCs; see definition on page 174). In the absence of such knowledge, a TPC could still allow environmental change up to a predetermined point at which managers must officially become concerned and the situation must then be reviewed. The outcome of such a review could either be a resetting of the TPC to allow for further change or else management of some form must be considered to prevent further change.

The new policy recommendation, as described here, was then formulated at a final meeting of the SANP staff held in Skukuza on 17 March 1997. The finalised policy document was presented on the Internet (http//www.parks-sa.co.za) for further public scrutiny, and on 31 October 1998 was also presented at a public meeting convened in Nelspruit. Almost unanimous public support was given at this meeting, the only objection coming from the animal rights group FALCON who felt that at least another 10 years was necessary before implementation, as new technologies may be forthcoming (such as contraception) to solve the problem in non-lethal ways (South African National Parks 1998). As there is no guarantee of this, and acknowledging the support of the majority of the people and organisations represented, the SANP Board approved the policy on 12 March 1999.

THEORETICAL BASIS OF THE NEW POLICY

The KNP is committed to a mission emphasising biodiversity in the widest sense (i.e. structure, function and composition across scales from genetic to landscape and even sub-continental),

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and makes specific mention of fluxes as part of this. The theoretical basis of quantifying and managing for biodiversity and flux has its origin in the emergent heterogeneity paradigm (e.g. Christensen 1997; Fiedler *et al.* 1997), but still has many unknown dimensions in practice.

Driving variables in savannas include nutrients, moisture, fire, herbivory and others (e.g. Wiens 1997). Elephant herbivory is considered particularly significant, as in some studies, elephants at high densities have been shown to negatively affect biodiversity (Cumming *et al* 1997, Western & Gichohi 1989). If there is variation in these driving variables over time and space, an ever-changing mosaic should be the outcome. The patches which result are seen as organised in a hierarchy of scales (Wiens 1997). If, for example, many levels of herbivory are naturally superimposed on a fire mosaic, then at certain scales even more diversity should result.

The intermediate disturbance hypothesis claims that the greatest species richness (and perhaps overall biodiversity) at one point in time and space is likely to result from intermediate levels of disturbance. At extreme levels of both low and high disturbance, there might indeed be fewer species, but certain species which are not favoured or are even absent at intermediate levels would very likely prosper. Thus, if the ecosystem can pass through various stages of disturbance in different places and at different times, the patchwork created might support the greatest overall diversity desirable in a natural system, though spatial variation can in many ways substitute for temporal variation and *vice versa*.

An equally important issue is the rate of change, as influenced by the pattern and intensity of disturbance - a rapidly increasing disturbance regime often has different ecological effects to a slowly increasing one, even if the final intensity is the same.

In recent years there has been increasing belief that most of the important changes in savannas are event-driven. They may occur only occasionally, when a certain co-occurrence of events (perhaps drought plus rapidly-rising levels of herbivory plus fire at a critical period, followed by good rain) brings about a particular shift from one state to another (perhaps an invasion of bush into grassland). Different ecological pressures then prevail which may stabilise the system in a new state for years or even decades. Current ecosystem theory takes cognisance of the likelihood of the existence of multiple stable states (Dublin 1995) as well as considering several

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other models of ecosystem dynamics. These differing ideas about how systems function span a range from the classical homogeneity/stability paradigms through to the relatively revolutionary disequilibrial notions (Behnke *et al.* 1993). Each of these models appears to have had some validity at some location and scale over some time span, our current understanding falling short of integration of these into a unified theory. Holling (1995) and others assert that by finding a particular apparent "winning recipe for ecosystem management" at a locality (the more homogeneous, seemingly the more dangerous) and keeping it static for too long, invariably leads to catastrophic change when an extreme event occurs, usually because of lack of resilience.

Scaling is a historically underrated issue and its understanding forms the crux of much new insight. Elephant impacts may operate at various scales, and much of what is presented here assumes that animals with such large body sizes, home ranges, walking ability and propensity for fast-increase are likely to create landscape-scale effects. Equally they may, perhaps at lower densities, create a mosaic of medium-scale (100's of metres to 10 km) effects with patches of riverine vegetation being "stripped completely" and other patches nearby not being touched. At the individual tree level, different fine-scale sequelae of their feeding on some parts and not others of the tree, might lead to habitat diversity for different insects. Time scales are equally important: long-term views often place shorter-term fluctuations into the perspective of making up the natural flux.

What does all this mean for management? Managers of natural systems are now entering an era where heterogeneity needs not only to be understood, but also implemented in some practical way. The outcome of this elephant management strategy is an attempt to meet this challenge, even if the scales at which the processes occur needs further understanding. The belief is, in the first place, that this management strategy will enhance biodiversity. Secondly, at the same time, it will provide an opportunity to learn by managing, a crucial element of adaptive management. Although much use will be made of the outcomes to learn more about future elephant management, it should not be seen primarily as an experiment - the options chosen are intended to meet the primary biodiversity objective of the KNP, rather than constitute any contrived or forceful experiment. Obviously, "unnatural over-heterogenisation" is possible, and is indeed practised by smaller ecotourism operations specifically to create habitat diversity for more

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species than might naturally occur at these sites. It is not the intention of the SANP to take the management of the KNP to this unnatural level, indeed where this has happened (artificial waterholes can lead to heterogenisation or homogenisation, obviously depending on the context) it is being reversed. In the same vein, the SANP would like to vary rates of change (thus increasing diversity, also through the differential resilience of different species and systems to different rates) but in a natural regime. The word "natural", as also embodied in the mission statement, thus provides an important cornerstone of this action. The TPCs, which will be continuously refined as knowledge, experience and hopefully wisdom grow, provide an attempt to outline the "envelopes" of acceptability to management. They are meant to delineate thresholds beyond which (it is believed) the system will have exceeded its inherent elasticity, and from which it may not have the ability to return to a healthy state.

The occurrence of the kinds of events which bring about changes, even drastic-seeming changes, should not be suppressed if they are natural, as they may contribute significantly to system resilience in the long-run (Holling 1995). KNP management should thus be geared to allowing these to take place. Management has to be capable of tracking ecosystem changes to see that they fall within TPCs, and may need to nudge the system in the "correct" direction if sustained trajectories towards (and believed to be going to exceed) TPCs are predicted. More drastic intervention may be needed when TPCs have been grossly exceeded due to modern human influence, though if the adaptive management and TPC-monitoring system is effective, this may not often be necessary. An understanding of the scales at which these different processes related to elephant impact occur, is extremely difficult to achieve, and will demand much research and modelling. Certainly, the SANP is trying to adopt a longer-term view, though realising the importance of perhaps shorter-term considerations such as the immediate tourism value of this unique species, as well as moral and ethical considerations.

CURRENT THINKING AND APPROACH TO ELEPHANT MANAGEMENT

Principles

This proposed new elephant management policy rests on three fundamental principles on which there was consensus at the meeting of 30 October 1996. These are:

i. In accordance with the new Vision Statement of the KNP, it is accepted that flux in ecosystems is natural and desirable as this contributes to biodiversity, and that this is

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probably also true for the elephant population.

ii. It is accepted that elephants are important agents of disturbance and as such create heterogeneity and thus contribute to biodiversity (Intermediate Disturbance Hypothesis). This was demonstrated in Amboseli National Park by Western & Gichohi (1989). This means that in the absence (or very low densities) of elephants, biodiversity will be negatively affected as no disturbance occurs. Excessive disturbances at high densities will also affect biodiversity negatively (these high and low end-points may also be shown to be desirable as it is believed that certain species will benefit from the conditions thus created, provided that they do not occur over a large area for too long).

iii. It is also accepted that elephant populations that are confined but not managed, will increase in number to a level where negative impacts on the system's biodiversity will result.

In recognising the above three principles, the following corollaries have to be considered:

i. To *maintain* an elephant population at a *high* level will require the culling and/or translocation of a larger number of individuals than when maintaining it at a lower level (this may have moral or ethical considerations).

ii. The *reduction* of an elephant population from a high level to a lower level will require the culling and/or translocation of a larger number of individuals than when maintaining it at a lower level (this may have moral or ethical considerations).

iii. Wherever possible, management of the elephant population should be conducted by non-lethal means (translocation, contraception, etc.) but that where these methods prove inadequate, culling must remain an option for use.

iv. When culling is necessary, only the most humane method available should be used.

Options for controlling elephant numbers other than culling

When or wherever elephant population control is considered necessary, the priority will always

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be to do so by non-lethal means. It is stressed that these options are not likely to fulfil the requirements needed to manage the KNP elephant population successfully. Where these options are not feasible, culling is currently the only practical option available to do so.

i. Translocation (live transfer)

Before the development of methods to translocate adult elephants, juvenile animals were captured at culling operations for translocation. Up to 1994, 1 339 juveniles were translocated in this way from KNP to other conservation areas. By 1994, methods enabling the live transfer of adult elephants had been developed and since then, 300 elephants in family units have also been translocated. With the advent of this technology, it is now believed that the translocation of juvenile animals is inhumane and therefore undesirable. This latter option will no longer be practised - only animals in intact family units will be transferred live out of the KNP.

Over the long term, the limited market for live animals will not provide the option of removing all excess elephants from the KNP through live transfer.

ii. Contraception

Chapter 6 reviewed the current state of contraception technology. This showed that it cannot yet offer a satisfactory method of population control in elephants (Whyte & Grobler 1997; Whyte *et al.* 1998).

Opposition to the contraception option has also been voiced by communities adjacent to KNP as they hold the belief that sustainable utilisation of the population should be practised. However, SANP should continue to support research on contraception technology with the hope that it will ultimately provide an additional practical and affordable option for the control of the KNP (and other) elephant populations.

THE NEW POLICY FOR MANAGING THE KNP ELEPHANT POPULATION

The new elephant management policy will differ from the old one in that the elephant population will be managed according to measured impacts on biodiversity rather than on absolute numbers of elephants. Different management options will be practised in different zones and aspects of biodiversity will be monitored. This management option will continue

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until there is clear evidence that the prevailing density of elephants is having a negative impact on some aspect of biodiversity which warrants concern. This point will be known as a "Threshold of Potential Concern" (TPC), which can defined as those upper and lower levels along a continuum of change in a selected environmental indicator which, when reached, prompts an assessment of the causes which led to such an extent of change, and results in either:

i. management action to moderate such cause(s), or
ii. re-calibration of the threshold to a more realistic or meaningful level.

Such TPCs are initially established at somewhat arbitrary levels on "best-available-knowledge-and-experience". It is absolutely necessary when deciding to use such TPCs that it must be accompanied by monitoring at appropriate intervals, and that there must be considerable understanding of the factors causing change in the parameter being monitored.

TPCs have the advantage that management has definite proactive objectives or parameters within which to manage a system, in contrast to previous practices which reactively managed events or processes to minimise or avoid crises. Nevertheless, TPCs should be constantly challenged as to their appropriateness or validity, and adaptively modified as knowledge and experience increase.

The appropriate TPCs for the management of the KNP elephant population have been set "widely" which will allow for considerable fluctuation in the populations of the respective management zones. The TPCs for elephant are given (in their current form) at the end of this elephant management policy proposal.

A zoning system for management of elephant impact

The KNP will be divided into six zones which will receive different treatments in terms of the management of their respective elephant populations (see Figure 24). These zones are:

i. two botanical reserves,
ii. two high-density elephant zones,
iii. two low-density elephant zones.

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In the high-density elephant zones the population will be allowed to increase (no culling or live removals) until there are indications that one or more of the Thresholds of Potential Concern (TPCs) have been reached or exceeded. It is expected that the elephant population of these zones will increases at 7% per year (see Chapter 5). In the low-density elephant zones the population will be decreased (through culling or live removals) until there are indications that low densities of elephants have induced change to a point that one or more of the TPCs have been reached or exceeded. This decrease will be achieved through the reduction of the populations in these zones by 7% per year. As the numbers of elephants in these zones are also expected to increase at 7% per year, it will mean the setting of a removal quota of 14% of the total recorded during the census to achieve a 7% reduction. In the Botanical Reserves medium densities are to be maintained. "Medium density" is here considered to be the density prescribed in the previous Masterplan (Joubert 1986) which was 0.35 elephants per km^2 (7 000 elephants in 20 000 km^2). Should one or more of the defined TPCs be reached or exceeded in these zones, then elephant numbers should be systematically reduced to negate this.

It is hoped that it will prove feasible for the management actions applied in the high- and low-density zones to be alternated, so that once a TPC has been reached or exceeded in any of the management zones, the alternate action will then be applied. High-density areas can then be treated as low-density zones and their populations systematically reduced while the elephant populations of the low-density zones can simultaneously be allowed to increase. While it is accepted in principle that this managed form of flux in the elephant population may prove to be beneficial and contribute to the maintenance of biodiversity in the KNP, it is felt that this should be demonstrated before it becomes permanently embodied in the elephant management policy.

There is some concern that increased elephant densities in the allocated zones may affect biodiversity in a way that is not reversible by a subsequent reduction in the elephant population. Theoretically a high elephant population may induce a decline in the population of some tree species, which may then not recover under the pressure of even a much lower elephant population. A more cautious approach will be followed - once the effects of an increased elephant population are better understood, this part of the policy should be reviewed.

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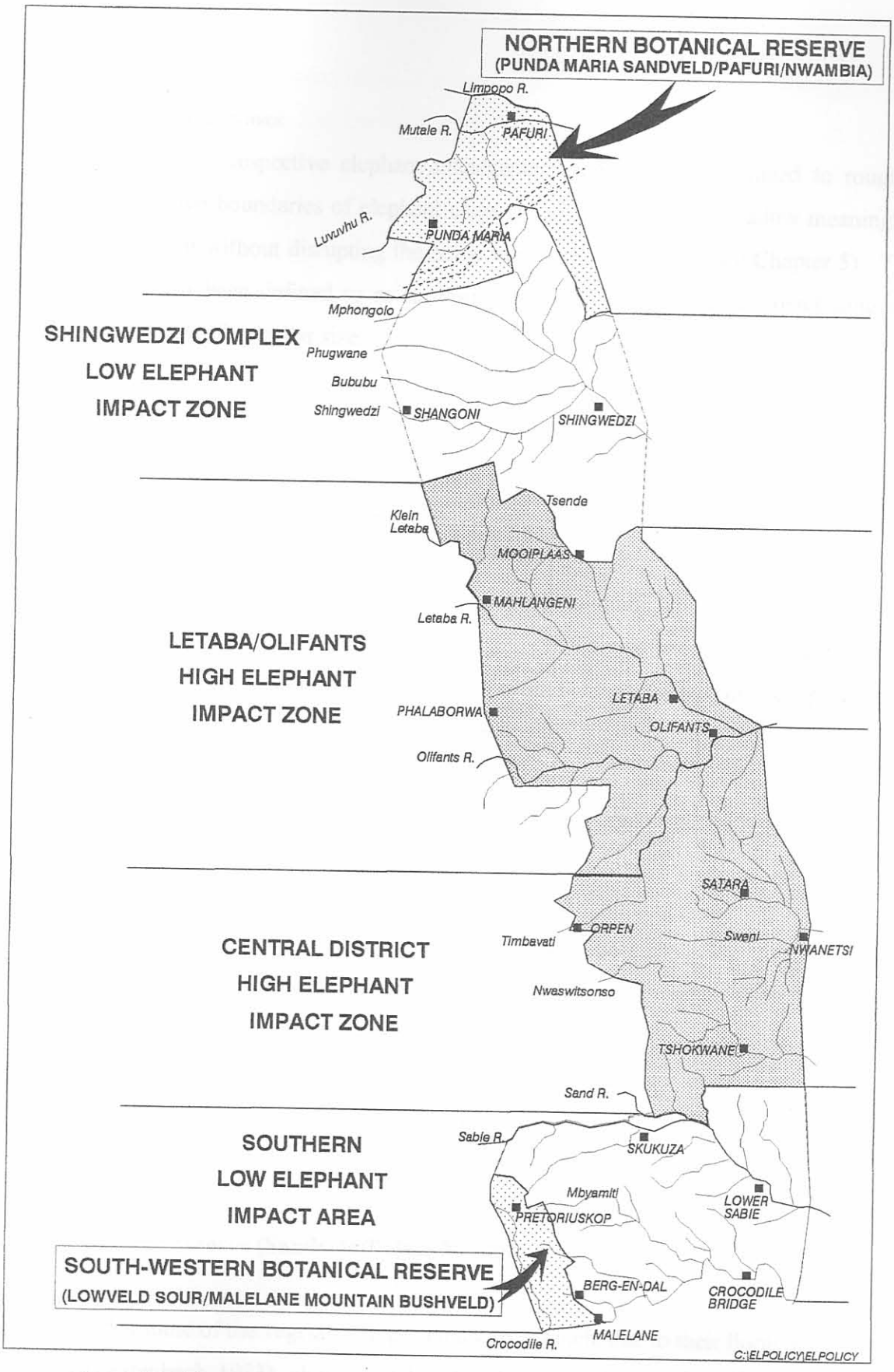


Figure 24: The zonation of the Kruger National Park for elephant management as proposed in the new elephant management policy (Whyte *et al.* 1999)

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Elephant management zones

The boundaries of the respective elephant management zones were designated to roughly conform to the known boundaries of elephant clans (Figure 17). This is to allow meaningful elephant management without disrupting the home ranges of these clans (see Chapter 5). The boundaries have also been defined so as to ensure that the four major zones (excluding the botanical reserves) are of a similar size.

The two high-impact zones have been placed adjacent to one another in the centre of KNP to establish a large core area of "no-management". The two low-impact zones then lie between the high-impact zones and the botanical reserves to obviate the problems of a hard edge between high densities of elephants and the botanical reserves. Once TPCs have been exceeded and the management actions in the respective high- and low-impact zones have been reversed, it is accepted that these problems will become a reality and will have to be addressed. But it may transpire that the elephants' home-ranges will remain intact through the management processes, and that little movement will occur across these boundaries.

The management of the Botanical Reserves will result from TPCs especially formulated for these areas (Pienaar *et al.* In prep.).

It may be expected that by reducing numbers in the two low-impact zones, the total number of elephants in the KNP will not be greatly influenced by the increases in the other two zones, keeping the total population at a manageable level. However, this is not expected to be the case as modelling of the responses of these zones to the planned management actions shows that the total KNP population will probably increase dramatically (see section on "Implementation of the Policy" below).

Northern Botanical Reserve (Sandveld/Pafuri/Nwambia)

Rationale

This area includes some of the vegetation types/landscapes which, due to their floral uniqueness in the KNP (Gertenbach 1983), should not be placed at risk of excessive elephant impacts (Pienaar *et al.* In prep.; Zambatis *et al.* 1997). The landscapes and vegetation types concerned

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are the *Colophospermum mopane* forest (Landscape 15 (Gertenbach 1983)), the *Adansonia digitata/Sterculia rogersii* area and the Nwambia sandveld communities. Whyte *et al.* (1996) have suggested that elephants may be partially responsible for a decline in the baobab population of this area.

Boundaries

The southern boundary extends from Dothole eastward along the Mananganana Firebreak to Magamba; then northward along the Shingwedzi/ Pafuri tarred road (HI-8) to Klopperfontein; then eastward along the Masokosa road to Masokosa Pan; then southward along the military service road; then turning eastward to the eastern boundary along the firebreak between Burning blocks 41 and 42. The other boundaries are constituted by the eastern, northern and western boundaries of the KNP. According to the KNP GIS system, the area of this zone is 1 552 km^2.

Elephant management

Although van Aarde *et al.* 1999 found that elephant densities declined in KNP after they exceeded 0.37 elephants/km^2, densities in the botanical reserves are to be initially maintained at a density of 0.35 elephants/km^2. This is the density that was prescribed in the earlier Masterplan for the Kruger National Park (Joubert 1986) at which it was felt that minimum impacts of elephants had been experienced. These densities will be monitored annually during aerial censuses and elephant movements in and out of the area will be monitored through the ongoing movement study using radio-collared animals. The number of elephants in the area should not exceed the prescribed density of 0.35 elephants per km^2 (i.e. 550). However, should one or more of the defined TPCs (see Table 16; Pienaar *et al.* In prep) be reached or exceeded, then elephant numbers should be systematically reduced (or increased) to negate this, as understanding indicates.

South-western Botanical Reserve (Lowveld Sour/Malelane Mountain Bushveld)

Rationale

This area also includes some of the vegetation types/landscapes of floral uniqueness in the KNP (Gertenbach 1983), which should not be placed at risk of excessive elephant impacts (Pienaar, Biggs, Venter & Whyte In prep.; Zambatis *et al.* 1997). These landscapes are the Lowveld

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Sour- and Malelane Mountain Bushveld (Landscapes 1 and 2).

Boundaries

The northern and eastern boundaries of this zone extend from Thlothloma on the western boundary eastward along the northern and eastern boundaries of Burning block 35; then along the northern and eastern boundaries of Burning block 57; then southward along the eastern boundary of Burning block 90; then following the western boundary of Burning blocks 103 and 87 as far south as Malelane Restcamp. The western boundary of the zone follows the western boundary of the KNP from Thlothloma southward to the Sigaas River mouth, and the southern boundary of the zone is the Crocodile River between Sigaas River mouth and Malelane. According to the KNP GIS system, the area of this zone is 700 km^2.

Elephant management

Elephant densities are to be maintained at a density of 0.35 elephants/km^2. These densities will be monitored annually during aerial censuses and elephant movements in and out of the area will be monitored through the ongoing movement study using radio-collared animals. The number of elephants in the area should not exceed 250. However, should one or more of the defined TPCs (Pienaar *et al.* In prep.) be reached or exceeded, then elephant numbers should be systematically reduced (or increased) to negate this, as understanding indicates.

Letaba/Olifants High Elephant Impact Zone

Rationale

It is the expectation of KNP managers that fluctuations in elephant numbers (as with all other biotic elements) will benefit natural ecological processes and other components of biodiversity, though this will require confirmation through the monitoring program (Pienaar *et al.* In prep). Elephant numbers in this zone will not be controlled. The intention is to allow elephant numbers to increase over a period of many years until one or more of the defined TPCs are reached or exceeded (as more than one may be reached concurrently). Following this, the zone may revert to a "low-density elephant zone" with systematic reduction of elephant numbers, thus inducing the desired population flux and the varying environmental impacts associated with it.

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Boundaries

The northern boundary of the zone will extend eastward from Busizi on the western boundary of the KNP along the northern boundary of Burning blocks 124 and 125; then southward along the eastern boundary of Burning blocks 124 and 129; then eastward along the southern boundary of Burning block 123 as far as the tarred road (HI-6); then southward along the tarred road (HI-6) as far as Mopani Restcamp; then eastward along the tourist road (S49) to the Nshawu Firebreak; then northward and eastward along the Nshawu Firebreak as far as the KNP's eastern boundary. The southern boundary of the zone extends eastward from Mangadyane on the western boundary (just north of Orpen) along the firebreak on the northern boundaries of Burning blocks 33, 34 and 30 as far as the Timbavati River; then northward along the Timbavati River to the Olifants River; then eastward along the Olifants River. The western and eastern boundaries of the zone are the western and eastern boundaries of the KNP. According to the KNP GIS system, the area of this zone is 4 883 km^2.

Elephant management

In this area elephant numbers will not be reduced either through culling or live removals. Numbers are expected to increase at a mean rate of approximately 7% per year. Monitoring of defined components of biodiversity (Table 16; Pienaar *et al In prep.)* will occur to determine the impacts of this increasing elephant density. The increase will be allowed to continue until one or more of the defined TPCs has been reached or exceeded. Appropriate management actions will then be debated by the KNP Standing Committee for Nature Conservation and all other interested or affected parties, with all the relevant data and reports under consideration.

It is hoped that the proposed trans-frontier conservation area (TFCA) in Mozambique (Braack 2000) will become a reality and that the removal of the fence on this zone's eastern boundary will allow a natural expansion of these elephants into Mozambique (Braack 2000).

Elephant densities will be monitored annually during aerial censuses and elephant movements in and out of the area will be monitored through the ongoing movement study using radio-collared animals.

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Central District High Elephant Impact Zone

Rationale

As with the Letaba/Olifants High Elephant Impact Zone, it is expected that fluctuations in elephant numbers (as with all other biotic elements) will benefit natural ecological processes and other components of biodiversity, therefore elephant numbers in this zone will not be controlled. The intention in this zone is also to allow elephant numbers to increase over a period of many years until one or more of the defined TPCs are reached or exceeded, following which this zone may revert to a "low-density elephant zone" with systematic reduction of elephant numbers, thus inducing the population flux desired by managers and the expected varying environmental impact associated with it.

Boundaries

The northern boundary of this zone is a common boundary with the Letaba/Olifants High Elephant Impact Zone's southern boundary; the southern boundary of this zone is a common boundary with the Southern Low Elephant Impact Zone's northern boundary. The eastern and western boundaries of the zone follow the eastern and western boundaries of the KNP. According to the KNP GIS system, the area of this zone is 4 149 km^2.

Elephant management

In this area, elephant numbers will not be reduced either through culling or live removals. Numbers are expected to increase at a mean rate of around 7% per year. Monitoring of defined components of biodiversity will occur to determine the impacts of this increasing elephant density. The increase will be allowed to continue until one or more of the defined TPCs has been reached or exceeded. Appropriate management actions will then be considered.

Elephant densities will be monitored annually during aerial censuses and elephant movements in and out of the area will be monitored through the ongoing movement study using radio-collared animals.

Shingwedzi Complex Low Elephant Impact Zone

Rationale

As with an increasing elephant population, it is expected that declining elephant numbers will

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also adversely affect biodiversity as the positive benefits of elephant impacts on heterogeneity are reduced. Elephant numbers will be systematically reduced at a rate of approximately 7% per year. By reducing the number of elephants at a consistent rate of 7% per year the actual number to be removed gradually declines each year so that the effects of the decline will diminish gradually.

It is hoped that the removal of the eastern boundary fence once the proposed TFCA has been established in Mozambique, will allow for some natural movement out of this zone which will reduce the number elephants to be artificially removed (either through culls or translocations).

The reduced elephant density in this zone will also act as a buffer between the Letaba/Olifants High Elephant Impact Zone and the Northern Botanical Reserve.

Boundaries

The northern boundary of this zone is a common boundary with the Northern Botanical Reserve's southern boundary; the southern boundary of this zone is a common boundary with the Letaba/Olifants High Elephant Impact Zone's northern boundary. The eastern and western boundaries of the zone follow the eastern and western boundaries of the KNP. According to the KNP GIS system, the area of this zone is 4 026 km^2.

Elephant management

Elephant densities will be reduced in this zone by 7% per year until one or more of the defined TPCs has been reached or exceeded. Appropriate management actions will then be considered. Elephant densities will be monitored annually during aerial censuses. Quotas for culling or live removals will be determined after the annual census result has become available. Elephant movements in and out of the area will be monitored through the ongoing movement study using radio-collared animals.

Southern Low Elephant Impact Zone

Rationale

As with the Shingwedzi complex low-density elephant zone, elephant numbers will be systematically reduced at a rate of approximately 7% per year. By reducing the number of

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elephants at a consistent rate of 7% per year the actual number to be removed gradually declines each year so that the effects of the decline will diminish gradually.

Boundaries

The western boundary of this zone is a common boundary the South-western Botanical Reserve. The southern boundary extends eastward along the Crocodile River from Malelane to the Mozambique border; the eastern border of the zone then extends northward along the Mozambique border to the Rietpan Firebreak; the northern border extends along the Rietpan Firebreak westwards to the Nwatindlopfu River; then southward along this river to its confluence with the Sabie River; then westwards along the Sabie River to the KNP's western boundary. According to the KNP GIS system, the area of this zone is 3 436 km^2.

Elephant management

Elephant densities will also be reduced in this zone by 7% per year until one or more of the defined TPCs has been reached or exceeded. Appropriate management actions will then be considered. Elephant densities will be monitored annually during aerial censuses. Quotas for culling or live removals will be determined after the annual census result has become available. Elephant movements in and out of the area will be monitored through the ongoing movement study using radio-collared animals.

THRESHOLDS OF POTENTIAL CONCERN FOR ELEPHANT IMPACT

Rationale

Table 16 lists TPCs for the high and low elephant impact zones, but not for the botanical reserves which need their own specific TPCs addressing plant community viability and optimum chance for rare species survival. The so-called "whole-park" measures given here thus refer to the whole KNP excluding the botanical reserves. TPCs for the botanical reserves have not yet been formulated (Pienaar *et al.* In prep.).

Any one TPC reached is meant to act as a significant warning sign on its own, and although evaluated in overall context with the rest, must be taken seriously in its own right.

The TPCs assume that any action then taken will significantly alter the predisposing

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environment which allowed that TPC to be reached. If at some stage in the future a very high density elephant population has evoked a TPC, the manner in which the populations are to be reduced will be of particular importance. Theoretically, there are many ways in which a large elephant population can be reduced. It might, if it were logistically possible, be reduced by 50% per year (fast removal), which may be necessary after a high-density phase to prevent further exceeding of the TPC. They might also be reduced by as little as 7% or less (slow removal). The TPCs given here presuppose fast removal. If slow removal is chosen, it will be important to tone down the TPCs somewhat to take into account the continued almost-as-high impact which will follow for many years after the peak is reached.

The relationship between the percentages given for within-zone and for the whole park TPCs (Table 16) may at first seem incongruous, given that the areas of the high and low zones are approximately equal (i.e. one might expect never to reach the whole-park TPCs). However, it is possible that only one of the two high (or for that matter low) zones may show severe changes, justifying the operational use of 30% (i.e. less than half of the 80%) as a TPC.

The list in Table 16 focuses on TPCs believed to be directly related to elephant, but other categories of TPCs (e.g. riparian health) may be exceeded due to elephant influence. These would obviously qualify as valid TPCs in their own right but are still in the formulation phase (Pienaar *et al.* In prep.).

Decision-making

Recommendations to the KNP Director as to appropriate actions for the management of elephants in the respective zones should be made by the KNP Standing Committee for Nature Conservation. The Standing Committee should co-opt appropriate senior management and research staff to appraise the results of the respective biodiversity monitoring projects and the annual elephant census results. Such appraisal should be done on an annual basis.

Table 16: Thresholds of Potential Concern for Elephants in the Kruger National Park

Criterion	Measure	Within-zone TPC	Whole-park TPC
Vegetation heterogeneity at coarse (mega) scale	Coverage (km^2) of landscape scale units (e.g. Gertenbach 1983) determined every 5 years. Result compared to any previous time, including historical.	80% change (cumulative) in the area of any landscape scale classification unit	30% change (cumulative) in the area of any landscape scale classification unit
Vegetation structure at community scale using size classes for a range of indicator woody species	Assume, e.g. 4 size classes. Then homogenisation is 90% dominance of any 2 size classes.	80% of all plots homogenous. Sensitive landscapes examined independently as well.	30% of all plots homogenous. Sensitive landscapes examined independently as well.
Woody canopy cover at community scale	% woody (within stratified landscapes, e.g. riparian) as determined from aerial photographs, done every 3 years	80% decline in canopy cover; specified increase with asymptote (see graph)	30% decline in canopy cover; specified increase with asymptote (see graph)
Rare, sensitive or characteristic (of the Lowveld) woody species (only in relation to elephant utilisation – short list)	Population size and structure fed into pv model	None, prepared to accept local loss or definite trend towards local loss of certain species (provided same species not declining seriously in lo/hi zones at the same time. i.e. species should NOT survive only in botanical reserves.)	99% probability of population persistence for next 100 years
Birds as surrogates for structural riparian health	Presence of species using reed beds, mudflats, litter, lower stratum, middle stratum, upper stratum	Because all perennial rivers are in or border on current high elephant areas, there is need for an in-zone TPC - when species from any category are no longer represented on any particular perennial river. Recolonisation thus assumed between zones.	Perennial rivers dealt with as within-zones issue per river; for seasonal rivers there will be a whole-park TPC, namely : when species from any category no longer represented in park as a whole - recolonisation from perennials rivers assumed.

Criterion	Measure	Within-zone TPC	Whole-park TPC
Birds as functional class representatives in riparian corridors (what about outside riparian corridors as well, wth own TPC's?)	Frugivores, gramnivores, insectivores (bark foragers, hawkers, leaf-gleaners), piscivores, raptors, nectarivores Frugivores, Gramnivores etc.	See above	see above
Invertebrate functional class representation	Ground and grass insects and spiders, tree dwelling insects and spiders, dung beetles, termites (harvester and macrotermes mounds), millipedes, pollinators.	When any class disappears from any zone (see proviso in whole-park TPC). Assumes recolonisation.	provided there are not serious concomitant decline of same classes in alternate zones.
Erosion/piosphere	RS classification – bare ground index	When affected area > unaffected area (ie. index >50%) or when affected area < 5% (latter to guarantee some eroded habitat in any zone)	when aggregated whole-park bare ground index less than 2.5% or > 25%

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THE IMPLICATIONS OF IMPLEMENTING THE NEW ELEPHANT MANAGEMENT POLICY

INTRODUCTION

In order to assess the implications of implementing the new elephant management policy on the elephant population, a spreadsheet model was developed to simulate the trends in the respective zones and also for the KNP as a whole.

METHODS

A simple spreadsheet model was constructed to calculate the number of elephants to be removed from each zone based on the management strategies listed for each of the six elephant management strategies described earlier. The starting point was the data derived from the aerial census of 1999. The populations in the botanical zones were reduced to and held at the prescribed density, those in the low-impact zones were reduced by 7% per year, while those in the high-impact (unmanaged) zones were increased by 7% per year. The projections were based on four assumptions which were:

i. that the elephants recorded in the respective management zones will remain in these zones and will not move into adjacent zones;
ii. that population growth rates will remain a constant 7% per year;
iii. that to achieve a 7% reduction in a population which is growing at 7% per year, a total of 14% of the animals recorded in that zone should be removed each year;
iv. that the management programs are implemented in the year 2000.

RESULTS

Scenario for the immediate future (year 2000)

The number of elephants to be removed from the respective zones' populations is given in Table 17. Since the prescribed limits for the botanical zones were exceeded by far, a large number of animals must be removed from these two zones. It is assumed that all of the excess elephants in the botanical reserves are removed in the first year while in the low-impact zones a 7% reduction is made. This gives a total of 963 elephants to be removed in the first year. This large quota results in a small decline after the first year. Thereafter, once the excess in the botanical zones has been removed, the numbers to be removed annually decline rapidly and the KNP population begins to increase (Table 18).

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Table 17: Population reduction quotas for the respective elephant management zones of the Kruger National Park in the year 2000 if the new elephant management policy were to be implemented.

Management Zone	Total counted in 1999	Limit	Total to be removed	Bulls to be removed	Br. Herds to be removed
Northern Botanical Reserve	901	550*	351	53	298
Northern Low Impact	1720		241	36	205
Northern High Impact	2665		0	0	0
Central High Impact	1524		0	0	0
Southern Low Impact	2001		280	42	238
Southern Botanical Reserve	341	250*	91	14	77
Total	9 152		963	144	819

* The limits for the botanical reserves are specified in the management policy.

** The respective quotas for bulls and breeding herds are 15% and 85% as these are the ratios at which they occur naturally.

Projections for the future

If the assumptions given above were to hold true, the population trends and the trends in the numbers of elephants to be removed can be projected into the future. These are given in Figure 25 and Table 18. Once the excess elephants have been removed from the botanical zones, the number to remove drops significantly in the second year (from 963 to 540). In subsequent years the management option for each zone is maintained until a hypothetical TPC is reached in the year 2020 (Figure 25). By this time the number to be removed has declined to just 170, while the KNP population as a whole has increased to almost 19 000.

Once a TPC has been reached, the management options for the high- and low-impact zones is reversed and once again the number of elephants to be removed increases dramatically due to the high numbers of elephants in the high impact zones which now need to be reduced.

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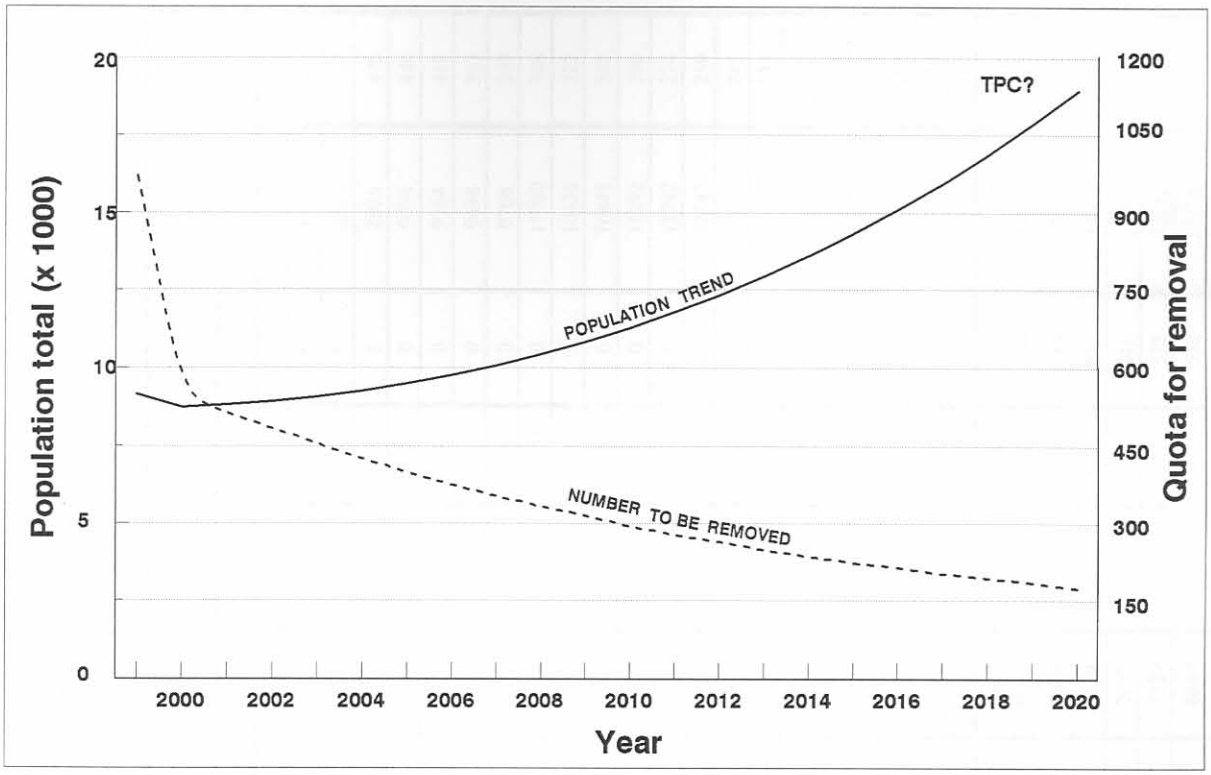


Figure 25: Expected elephant population trends and numbers to be removed from the population after the implementation of th new elephant management policy. The assumptions are that the population is growing at 7% per year, and that the elephants remain in the respective management zones.

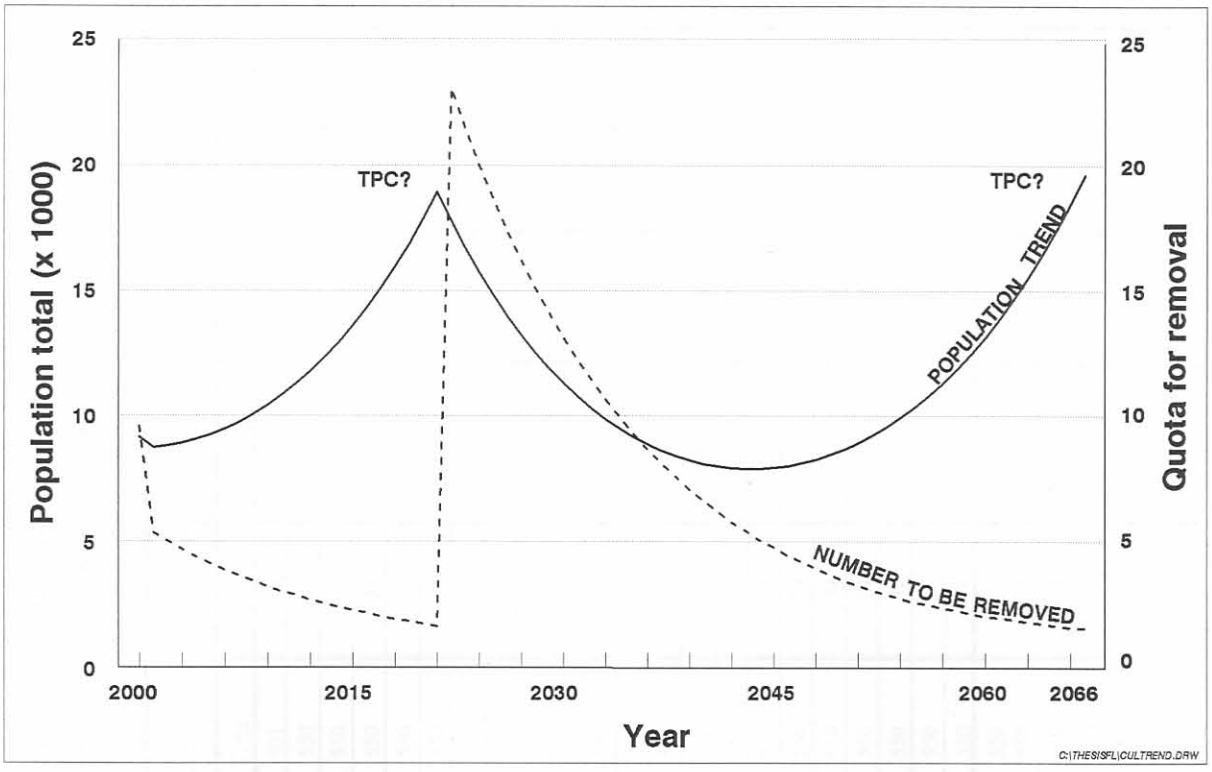


Figure 26: Expected elephant population trends and numbers of elephants to be removed from the population before and subsequent to reaching a TPC. The assumptions are that the population is growing at 7% per year, and that the elephants remain in the respective management zones.

Table 18: Expected elephant population trends in the Kruger National Park and its respective elephant management zones subsequent to the implementation of the new elephant management policy.

Year	Northern Botanical Reserve		Southern Botanical Reserve		Northern Low-impact		Southern Low-impact		Northern high-impact		Southern high-impact		Total population	Total quota
	Total	Quota	Total	Quota	Total	Quota	Total	Quota	Total	Quota	Total	Quota		
1999	901	351	341	91	1720	241	2001	280	2665	0	1524	0	9152	963
2000	550	39	250	18	1600	224	1861	261	2852	0	1631	0	8743	540
2001	550	39	250	18	1488	208	1731	242	3051	0	1745	0	8814	507
2002	550	39	250	18	1383	194	1610	225	3265	0	1867	0	8925	475
2003	550	39	250	18	1287	180	1497	210	3493	0	1998	0	9074	446
2004	550	39	250	18	1197	168	1392	195	3738	0	2137	0	9264	418
2005	550	39	250	18	1113	156	1295	181	3999	0	2287	0	9494	393
2006	550	39	250	18	1035	145	1204	169	4279	0	2447	0	9766	369
2007	550	39	250	18	962	135	1120	157	4579	0	2619	0	10080	348
2008	550	39	250	18	895	125	1041	146	4899	0	2802	0	10438	327
2009	550	39	250	18	832	117	968	136	5242	0	2998	0	10841	308
2010	550	39	250	18	774	108	901	126	5609	0	3208	0	11292	290
2011	550	39	250	18	720	101	838	117	6002	0	3432	0	11792	274
2012	550	39	250	18	670	94	779	109	6422	0	3673	0	12343	259
2013	550	39	250	18	623	87	724	101	6872	0	3930	0	12949	245
2014	550	39	250	18	579	81	674	94	7353	0	4205	0	13610	231
2015	550	39	250	18	539	75	627	88	7868	0	4499	0	14332	219
2016	550	39	250	18	501	70	583	82	8418	0	4814	0	15116	208
2017	550	39	250	18	466	65	542	76	9008	0	5151	0	15966	197
2018	550	39	250	18	433	61	504	71	9638	0	5512	0	16887	187
2019	550	39	250	18	403	56	469	66	10313	0	5897	0	17882	178
2020	550	39	250	18	375	52	436	61	11035	0	6310	0	18955	169
2021	550	39	250	18	401	0	466	0	10262	1437	5869	822	17798	2314
2022	550	39	250	18	429	0	499	0	9544	1336	5458	764	16730	2156
2023	550	39	250	18	459	0	534	0	8876	1243	5076	711	15744	2009
2024	550	39	250	18	491	0	571	0	8254	1156	4720	661	14837	1872
2025	550	39	250	18	526	0	611	0	7677	1075	4390	615	14003	1745
2026	550	39	250	18	562	0	654	0	7139	999	4083	572	13238	1627
2027	550	39	250	18	602	0	700	0	6640	930	3797	532	12538	1517
2028	550	39	250	18	644	0	749	0	6175	864	3531	494	11899	1415
2029	550	39	250	18	689	0	801	0	5743	804	3284	460	11317	1320
2030	550	39	250	18	737	0	857	0	5341	748	3054	428	10789	1231

Year	Northern Botanical Reserve		Southern Botanical Reserve		Northern Low-impact		Southern Low-impact		Northern high-impact		Southern high-impact		Total population	Total quota
	Total	Quota	Total	Quota	Total	Quota	Total	Quota	Total	Quota	Total	Quota		
2031	550	39	250	18	789	0	918	0	4967	695	2840	398	10313	1149
2032	550	39	250	18	844	0	982	0	4619	647	2641	370	9886	1072
2033	550	39	250	18	903	0	1050	0	4296	601	2457	344	9506	1001
2034	550	39	250	18	966	0	1124	0	3995	559	2285	320	9170	935
2035	550	39	250	18	1034	0	1203	0	3715	520	2125	297	8876	874
2036	550	39	250	18	1106	0	1287	0	3455	484	1976	277	8624	816
2037	550	39	250	18	1184	0	1377	0	3213	450	1838	257	8412	763
2038	550	39	250	18	1266	0	1473	0	2988	418	1709	239	8237	714
2039	550	39	250	18	1355	0	1576	0	2779	389	1589	223	8100	668
2040	550	39	250	18	1450	0	1687	0	2585	362	1478	207	8000	625
2041	550	39	250	18	1551	0	1805	0	2404	337	1375	192	7935	585
2042	550	39	250	18	1660	0	1931	0	2236	313	1278	179	7905	548
2043	550	39	250	18	1776	0	2066	0	2079	291	1189	166	7911	514
2044	550	39	250	18	1901	0	2211	0	1934	271	1106	155	7951	481
2045	550	39	250	18	2034	0	2366	0	1798	252	1028	144	8026	452
2046	550	39	250	18	2176	0	2531	0	1672	234	956	134	8136	424
2047	550	39	250	18	2328	0	2709	0	1555	218	889	125	8282	398
2048	550	39	250	18	2491	0	2898	0	1446	202	827	116	8463	374
2049	550	39	250	18	2666	0	3101	0	1345	188	769	108	8681	352
2050	550	39	250	18	2852	0	3318	0	1251	175	715	100	8937	331
2051	550	39	251	18	3052	0	3550	0	1163	163	665	93	9232	313
2052	550	39	252	18	3266	0	3799	0	1082	151	619	87	9567	296
2053	550	39	253	18	3494	0	4065	0	1006	141	575	81	9944	281
2054	550	39	254	18	3739	0	4349	0	936	131	535	75	10363	266
2055	550	39	255	18	4000	0	4654	0	870	122	498	70	10827	253
2056	550	39	256	18	4280	0	4980	0	809	113	463	65	11338	241
2057	550	39	257	18	4580	0	5328	0	753	105	430	60	11898	229
2058	550	39	258	18	4901	0	5701	0	700	98	400	56	12510	219
2059	550	39	259	18	5244	0	6100	0	651	91	372	52	13176	209
2060	550	39	260	18	5611	0	6527	0	605	85	346	48	13900	200
2061	550	39	261	18	6004	0	6984	0	563	79	322	45	14684	192
2062	550	39	262	18	6424	0	7473	0	524	73	299	42	15532	184
2063	550	39	263	18	6873	0	7996	0	487	68	278	39	16448	177
2064	550	39	264	18	7355	0	8556	0	453	63	259	36	17437	171
2065	550	39	265	19	7869	0	9155	0	421	59	241	34	18501	165
2066	550	39	266	19	8420	0	9796	0	392	55	224	31	19648	159

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This also results in a decline in the overall population which persists for about 20 years (Table 18 and Figure 26). At this time, the number of elephants in the "new" high-impact zones has built up to a level where the 7% increase exceeds the number to be removed from the "new" low-impact zones and population begins another growth cycle. This will continue until another TPC is reached sometime in the future.

Possible future options

At the time of writing, the demand for live elephants was very limited and the expectation is that the SANP will only be able to annually dispose of about 30 animals from breeding herds and 30 bulls through live transfer. As contraception is not yet available as a tool for elephant management, culling will have to be the method used to dispose of the majority of the quota. While this limits the opportunities for the management of the KNP elephant population by non-lethal means at present, this situation will in all likelihood change once the proposed new TFCA with Mozambique has been established (Braack 2000). This could allow for the removal of the fence between these two national parks (although the bovine tuberculosis (BTB) problem in KNP would have to be taken into consideration), and will offer considerable opportunities for natural recolonisation and translocations, particularly once the annual quotas have declined after a few years (Table 18). It is conceivable that all of KNP's excess elephants could be managed non-lethally in this way. While this may seem to be the best option, it will be extremely expensive and would require extensive donor funding. It must however be remembered that the TFCA will only offer a temporary solution, as there will also be a limit to the number of elephants that it could accommodate.

EVALUATION OF THE NEW POLICY

It is clear that SANP made a sincere effort to develop this new policy in the most transparent manner, as it invited and involved people from interested and affected parties in the development (workshopping) process. The result has been that, in its current form, the policy has satisfied a wide diversity of opinion from academics to some animal welfare groups. While I was an integral part of the development process (Whyte *et al.*1997; Whyte *et al.* 1999) and fully support its earliest implementation, I believe that some problems will arise in future which are

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likely to ensure that this policy will not be a long-standing one.

Assumptions in the policy which may not be valid

Biodiversity implications

There is as yet no evidence to support the assumption that fluctuating levels of elephant density will promote the long-term maintenance of biodiversity in the "conservation islands" which most national parks have now become. The intermediate disturbance hypothesis has, to a certain degree, been substantiated in the case of elephant disturbances (Western and Gichohi 1989), and while it is probably true that at the extremes of either increasing or decreasing levels of elephant disturbance, other species would be favoured, the question arises: Which are these species and where will come from? Are they species which already occur in low densities in KNP which would be favoured by the changes, or are they indigenous species not normally occurring but which could expand their ranges into KNP to capitalise on the changed habitat conditions? In the case of bird species this latter may be possible but for most other species, natural colonisation or recolonisation may have become an insurmountable problem in the modern age.

Where a plant species has been significantly reduced in population size through elephant utilisation (such as baobabs in Tsavo East (Leuthold 1977)), or as might be the case when a TPC is reached in KNP, it may not be able to recover even when elephant numbers have been reduced. The elephants remaining may still be able to eradicate the few that are left. And where species have been eliminated from ecosystems by extreme elephant habitat modification as has been the case with bushbuck (*Tragelaphus scriptus*) and Lesser kudu (*Tragelaphus imberbis*) in Amboseli National Park, Kenya (Western & Gichohi 1989), recolonisation may be impossible (even if elephant numbers declined dramatically) as a source population in close enough proximity may not exist. Instead of favouring biodiversity, species could thus be lost which is directly contrary to the stated objectives of the policy.

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Elephant home ranges

The elephant movement study in KNP showed that matriarchal groups have a high degree of fidelity to their home ranges (see Chapter 5). Based on this, and the knowledge acquired on the dimensions of their respective home ranges, the boundaries of the respective management zones were assigned. But the assumption that this situation will persist as relative densities change subsequent to the implementation of the new policy may be flawed. There are two further possible outcomes:

- that elephants will move from the high- to the low-impact zones as resources diminish in the high-impact zones;
- that elephants will move from the low- to the high-impact zones to escape the traumas of management.

In the first case, elephants moving out of the high-impact zone will neutralise the objectives of the policy. All that will have happened is that "source-sink" zones have been created where elephants moving out of the high-impact zone must be culled in the low-impact zones. This would also mean the removal (by culling or otherwise) of much larger numbers of elephants. "High- and low-impact zones" will thus not be an attainable objective, requiring the formulation of an entirely new policy.

In the second case, elephants moving from low- to high-impact zones will work in favour of the policy's objectives, as the hoped-for densities in the respective zones will be achieved more easily, requiring minimal numbers to be culled (this is a stated objective of the policy). A potential drawback of this however is that TPCs will be reached sooner, shortening the elephant population fluctuation period, and thus minimising the "recovery time" for vegetation in the low-impact zones.

Foreseen problems with the Policy

Dissimilar time scales between the reaching of TPCs in high- and low-impact zones

It is likely that the negative consequences for biodiversity arising in the low-impact zones from too few elephant will be a longer-term processes than those arising in the high-impact zones

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from too many. The elephants' positive roles for biodiversity may include seed dissemination, control of bush encroachment and making of browse available to other browsers through pushing over trees and breaking of branches. In the absence of elephants, seed dispersal for some species may be compromised, bush encroachment may occur and browse shortages may become limiting for some browsing species. But all of these processes are likely to take many years before they reach TPC levels resulting in the necessity to switch management regimes in the high-impact zones before the low-impact zones are "ready". The reversal of the strategies (high-impact becoming low-impact and vice-versa) will then follow the same trend - TPCs will be reached in the new high-impact zones well before those in the new low-impact zones. These zones will thus never be afforded the desired rest periods. This will ultimately result in park-wide TPCs being exceeded. What then? Once again a new policy will need to be formulated.

High impact zones versus biodiversity and agriculture

The reversal of the strategies (High-impact becoming low-impact and vice-versa) will also mean that high-impact zones will directly adjoin both botanical reserves as well as the agricultural areas along the Crocodile River. As elephant numbers build up, they are likely to place increasing pressure on both, resulting in increased management of the elephants which will be contrary to the objectives of the policy.

Capacity to cull or translocate large numbers of elephants

The capacity of the Game Processing Plant (abattoir) is limited to about 850 – 1000 elephants per year. At current levels the demand for live elephants is unlikely to exceed more than 100 per year. As populations build in the high-impact zones, the number of elephants which will have to be removed once a TPC is reached, may exceed this capacity. This may force managers into a situation where management actions (population reduction) must be instituted before the TPC is reached, as it would be tactically disastrous to allow the elephant population to reach "unmanageable" proportions. This consideration may affect the option of management through TPCs.

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Expected positive outcomes

Monitoring programs and TPCs as a form of management

The management of natural areas through TPC controlled monitoring and management programs is a new concept pioneered for this policy. The system need not be applied only to elephant management, but in all areas where expected ecological impacts or changes may be anticipated. Any successes achieved by this concept as outlined in this policy will almost certainly lead to a much wider usage of the concept in SANP and other conservation organisation elsewhere in Africa.

The value of the learning process

The real value of this policy will lie in what will be learned about actual impacts of increasing (and declining) elephant populations on biodiversity through the monitoring program. This will be of particular interest to all elephant managers in Africa. No policy can be "cast in stone" and it is inevitable that this one will be modified or even completely reformulated through lessons learned.

How may the policy change in future?

It seems certain that the dissimilar time scales between the reaching of TPCs in high- and low-impact zones as discussed above will ultimately necessitate another reformulation of the policy. If this should be the case, it would be wise for management to reconsider the policy at the time the first TPC is reached. Consideration of the fact that the switching of the strategies in the high- and low-impact zones respectively may lead to park-wide TPCs being reached or even exceeded, with the corresponding threat of possible losses of species from the system. A reformulation of the policy will probably be necessary. I foresee two possible outcomes, depending on what has been learned.

Modification of the current policy

A logical refinement of the policy may be to retain the respective management zones as they

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have been defined without the switching of management strategies. i.e. allow the elephants permanent access to these zones without management. Some of the elephant related TPCs could be disregarded but the monitoring programs would be continued. Advantages of this reformulation would be:

- The current high-impact zones are mainly the mopani areas which probably contribute least to the KNP's biodiversity.
- The communities and species of particular concern are already in the botanical reserves. The low-impact zones would act is "intermediate refuges" for species intolerant of high elephant densities. All known species are represented elsewhere in the KNP in either the botanical reserves or low-impact zones.
- The reaching of park-wide TPCs from high densities of elephants would be precluded.
- The trends as indicated in Table 18 show that the number of elephants to be removed (quota) declines continuously. If the assumptions hold, then in 22 years this quota is reduced to as little as 170 animals. This number could easily be handled through translocations and (if necessary) minimised culling.
- The heavily impacted elephant zones would serve as prime tourist areas, as well as "points of reference" – examples of the scope of elephant "damage" as justification for their management elsewhere.
- Should the TFCA in Mozambique become established and the eastern boundary fence be removed, the high-impact zones will adjoin the area in Mozambique allowing for natural recolonisation and a natural reduction in KNP elephants. The switching of management strategies would place one high-impact zone far removed from Mozambique, precluding this opportunity.

A reversion to a policy similar to the old one

The Intermediate Disturbance Hypothesis has to a certain degree been substantiated for elephant disturbances (Western and Gichohi 1989). It may be that the previous policy (Joubert 1986), which held elephant numbers at a relatively low density will prove to be more successful at maximising biodiversity than one promoting elephant population fluctuations. In the 28 years

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that this policy was adhered to (1967-1994), no species is known to have been extirpated from KNP through elephant related impacts. A reversion to this or a similar policy may therefore be considered.

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SUMMARY

Various aspects of the conservation management of the elephants in Kruger National Park were investigated. The thesis covers most of the important aspects which may have influenced the population, starting with the early history of the population and finishing with a view to the future of the population under a new elephant management policy.

In contrast to previous historical accounts which suggested that elephants must have been abundant in the KNP area before the arrival of Europeans and their firearms, the evidence presented here, from a study of baobabs and a literature survey, suggested that this may not have been not the case. The evidence from baobabs was largely indirect but suggested that the prevailing abundance and population structure could not have been exposed to high densities of elephants (such as has occurred elsewhere in Africa) at any time during the life spans of the individuals currently in the population. The scarcity of elephants in the rock art of the San (Bushmen) in KNP compared to their popularity elsewhere in South Africa also suggests that these animals were rare during the San era. The earliest Europeans (de Cuiper) penetrated the KNP area in 1752 but found that the indigenous people they encountered did not consider the area as an "ivory area" but were told that ivory was plentiful in Zimbabwe. Later pioneers (Louis Trichardt and Joâo Albasini) could also provide no evidence of high densities of elephants. The writings of the later hunters show that those who hunted elephants did not do so in the KNP area, while those that did hunt there did not shoot elephants.

After the proclamation of the area as the Sabi Game Reserve and later the Kruger National Park, the elephant population increased unchecked and recolonisation of the entire area occurred. This process is documented and recolonisation rates estimated. Elephants were recorded for the first time in the central area of KNP in 1905, and the recolonisation process took until 1945 to reach the northern boundary and to 1958 to reach the south-western corner. The growth of the population up to the implementation of management actions is reviewed.

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Management in the form of fencing and culling was initiated in the 1960's. The management policy of the time is reviewed. The census and culling techniques are described and evaluated. The census technique has remained standardised since 1967. The estimates of the census' precision ranged between 12.1% and 7.3% of the expected result. Culling techniques changed from the use of the compound scoline (succinylcholine chloride) to shooting with a heavy calibre rifle, as scoline was shown to cause death through asphyxiation, which is considered inhumane.

The policy's objective was to maintain the elephant population at around 7 000. The history of management under this policy is recorded. The numbers of elephants removed in this process between 1967 and the present was between 16 and 1 846 annually, making up a total of 16 520 elephants.

The observed rate of increase ($\bar{r}$) of the population was estimated from the annual census results. Annual estimates of $\bar{r}$ showed a declining trend which is thought to be related to fencing. The last of KNP's boundaries was fenced in 1976 and between 1967 and 1976, the mean $\bar{r}$ was 0.104, the high value resulting from immigration from Mozambique. Between 1976 and 1994 the population was confined and the mean $\bar{r}$ was 0.066. This is regarded as the natural rate of increase as it was not influenced by immigration or emigration. The western boundary fence was removed in 1994 and between then and 2000, $\bar{r}$ declined further to 0.015. This is thought to result from emigration to the private reserves to the west.

The mean calving interval (MCI) was calculated at 3.99 years from the respective proportions of pregnant and non-pregnant cows examined at culls. Cull data also allowed an estimate of the proportion of breeding cows in the population. These two estimates in turn allowed an estimate of the potential rate of increase of 0.098, which is the rate of increase if no mortalities were to occur. The difference between the observed and potential rates of increase gave an estimate of the mean annual mortality of 3.2%.

Movements of 29 adult elephants were studied using radio telemetry. Home ranges were determined for both 100% Minimum Convex Polygons (MCP's) and 90% MCP's. The

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recorded home ranges (100% MCP's) varied in size between 86 km^2 and 2 776 km^2 with a mean of 880 km^2, while the 90% MCP's ranged from 45 km^2 to 1 805 km^2, with a mean of 523 km^2. Some of the cows occupied very similar ranges and were probably of the same "clan", but the 90% MCP's showed distinct separation of other cows who were clearly from different clans. Movements suggested that these cows have a high degree of fidelity to their home ranges and that although movements may be induced by the disturbance of culls, they do not leave these ranges. This allowed the designation of boundaries of management zones in the new elephant management policy between these home ranges, as it is expected that these will be maintained once this new policy is implemented.

Aerial censuses provided data for an analysis of culling on the dynamics of the population. The KNP was divided by management into four zones. A full year's cull was taken from one of these zones per year on a rotational basis. Responses of sub-populations in these zones were monitored to determine how post-culling densities affect population growth rate. The analyses suggest there may be an alternative management strategy for the elephants in KNP. From these analyses it appears that numerical changes in elephant sub-populations in KNP are density dependent. At densities >0.374 elephants/km^2 the population tended to decrease, i.e. that in KNP density dependence of population growth rate only starts operating at densities greater than 0.37 elephants/km^2. This density is equivalent to an elephant population of very nearly 8 000 for KNP, and was thus within the limits set for the population by earlier KNP managers. However, these analyses were conducted on the sub-population level and changes in population size for a given region may have resulted from intra-population movements rather than changes in demographic variables.

In the wake of the moratorium placed on culling in KNP since 1994, contraception research was encouraged as a non-lethal means of population control. The dilemmas of elephant management were presented and a spreadsheet model was developed to investigate the logistics of a contraception operation. This showed that to ensure zero population growth, the average calving interval would have to be reduced to about 12 years,

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or about 75% of all cows >12 years. In KNP this equates to about 2 250 cows which would have to be under treatment. Furthermore, a zero population growth rate would only be attained after 11 years of treatment because in that 11-year interval, females born before the use of the contraceptives would steadily be recruited into the breeding population. The final management effort would require ≅ 4 000 animals to be under treatment. Through the model, a numerically simpler means of limiting population growth was identified. The killing or sterilization of 250 pre-breeding cows would achieve the same goal.

An assessment of two contraception techniques was made. The methods were the "immuno-contraception" method using porcine zona pellucida immuno-contraceptive vaccine (pZP), and hormonal control through surgical subcutaneous insertion of oestradiol-17ß implants. These techniques each had certain potential problems associated with them such as social disruption, threats to the health and welfare of the treated animals and/or their calves, and behavioural aberrations. The oestradiol treatment proved unacceptable to managers for various reasons. A state of false oestrus was experienced by treated cows resulting in harassment by bulls. This caused separation of the cows from their calves and matriarchal groups. Three calves from the 10 treated cows disappeared while none disappeared from the pZP treated group. Contraception was achieved but treated cows appeared to have been permanently sterilised. The pZP program achieved some successes and no behavioural problems were observed. This method holds promise for smaller populations.

The process of developing the new elephant management policy is recorded and the new policy presented. This policy defines six management zones in KNP. Two of these are botanical reserves where rare plants and plant communities are to receive management priority. The elephant populations of two of the remaining zones (low-impact zones) are to be reduced annually by 7% to induce a gradual decline. In the final two zones (high-impact zones), no management will take place, and it is anticipated that numbers will increase at the observed rate of increase of around 7% per year. The expectation is that both the high and low densities induced in these respective zones will ultimately have negative consequences for biodiversity. Changes will be monitored through a biodiversity

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monitoring program. Acceptable limits to these changes will be set in the form of "Thresholds of Potential Concern" (TPCs). Should one or more of these be reached or exceeded, the prescribed management option will be reversed and low-impact zones will become high-impact zones and *vice versa*. Population trends under this new policy were modeled, showing that numbers to be removed from the population decline, while the population itself increases. After a TPC is reached, numbers to be removed will increase dramatically but decline again over time, while populations decline initially but will then enter a phase of increase again. Numbers and time scales are dependent upon when and at what elephant density the TPC is reached.

A personal evaluation of this new policy is presented.

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APPENDIX 1: A DEVICE TO DETERMINE ELEPHANT (AND OTHER MAMMAL) FOETAL CONCEPTION AND BIRTH DATES

This part of the thesis was compiled from a paper which describes this device (Whyte 1986). It was devised before hand-held computers were available for use in the field, and proved useful in determining elephant foetal conception and birth dates.

The calculation of foetal age is a simple matter even on a hand-held electronic calculator but in the field, the determination of conception and birth dates can be a laborious process if there is no access to a suitably programmed computer. To determine the conception date of a near full-term foetus of a species with a long gestation time (e.g. elephant) involves a lengthy process of counting backward through a calendar for the relevant number of days until the conception date is determined. A similar problem arises when determining the birth date of a young foetus. The process is laborious, time-consuming and prone to error. The device described here eliminates these problems. It is simple, easy to use and accurate, and has been calibrated for elephant, buffalo, hippopotamus and impala.

Huggett & Widdas (1951) found that the equation $W^{1/3} = a(t-t_o)$, where W is foetal mass, a is the specific growth velocity and t_o is the intercept of the linear growth line with the time (x) axis, gave an adequate estimation of mammalian foetal age (age of foetus since conception). The authors stated however, that as t_o was an arbitrary estimate, errors of up to 10% could be expected when growth velocities and foetal ages are calculated. Attention to this limitation was again drawn by Guy (1983), but in spite of this limitation, the Huggett & Widdas equation is still widely used to determine foetal age and thus also conception and birth dates.

To assemble the device, cut out its three elements as shown in Figure 27. Glue or staple the calendar disc (a) onto a piece of soft-board or robust cardboard. For best results a photocopy of Figure 1 made on overhead transparency film should be used as it is robust and transparent. Through the centre points of the two discs and the indicated point on the "collection-date pointer" (b), pin the three elements together with the foetal-age disc (c) on top, and the collection-date pointer between the two discs.

Set the collection-date pointer to the date on which the foetus was sampled. From the foetal

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weight and using the Huggett & Widdas formula, estimate the foetal age in days. Turn the foetal-age disc until the foetal age is directly opposite the arrow on the collection-date pointer. Read the conception and birth dates off the calendar-disc as indicated by the relevant arrows on the foetal-age disc.

When reading off these dates, care must be taken to ensure that the correct year is ascribed. This is particularly important in the case of elephant where the 660 day gestation time makes it possible that there can be a two year difference between the year of collection and the year of conception or birth.

Gestation times and average birth weights for the four species are given in Table 18. The variables for the Huggett & Widdas equations for these species are also given for convenience. The variables given for elephant are those of Craig (1984) who revised the Huggett & Widdas equation for elephant.

Although it may seem pedantic to try to determine these dates to the exact day when Huggett & Widdas themselves concede errors of up to 10% in their method, this is how the formula is applied in practice. Whether by back and forward counting on a calendar, or whether these dates are calculated by computer, specific conception and birth dates are ascribed, and as long as the method used is standardised, comparisons can be made between or within populations either spatially and/or temporally.

Table 18. Birth weights, gestation times and specific variables of the Huggett & Widdas formula for the four species of herbivores.

Species	Birth Weight (g)	Gestation time (days)	t_o *	a *	References
Elephant	120 000	660	138	0.0945	Kenneth & Ritchie (1953); Perry (1953); Craig (1984)
Buffalo	45 000	340	68	0.131	Sinclair (1977)
Hippopotamus	42 000	240	48	0.181	Smuts & Whyte (1981)
Impala	5 370	196	39	0.112	Fairall (1969)

* Variables from the Huggett & Widdas (1951) formula.

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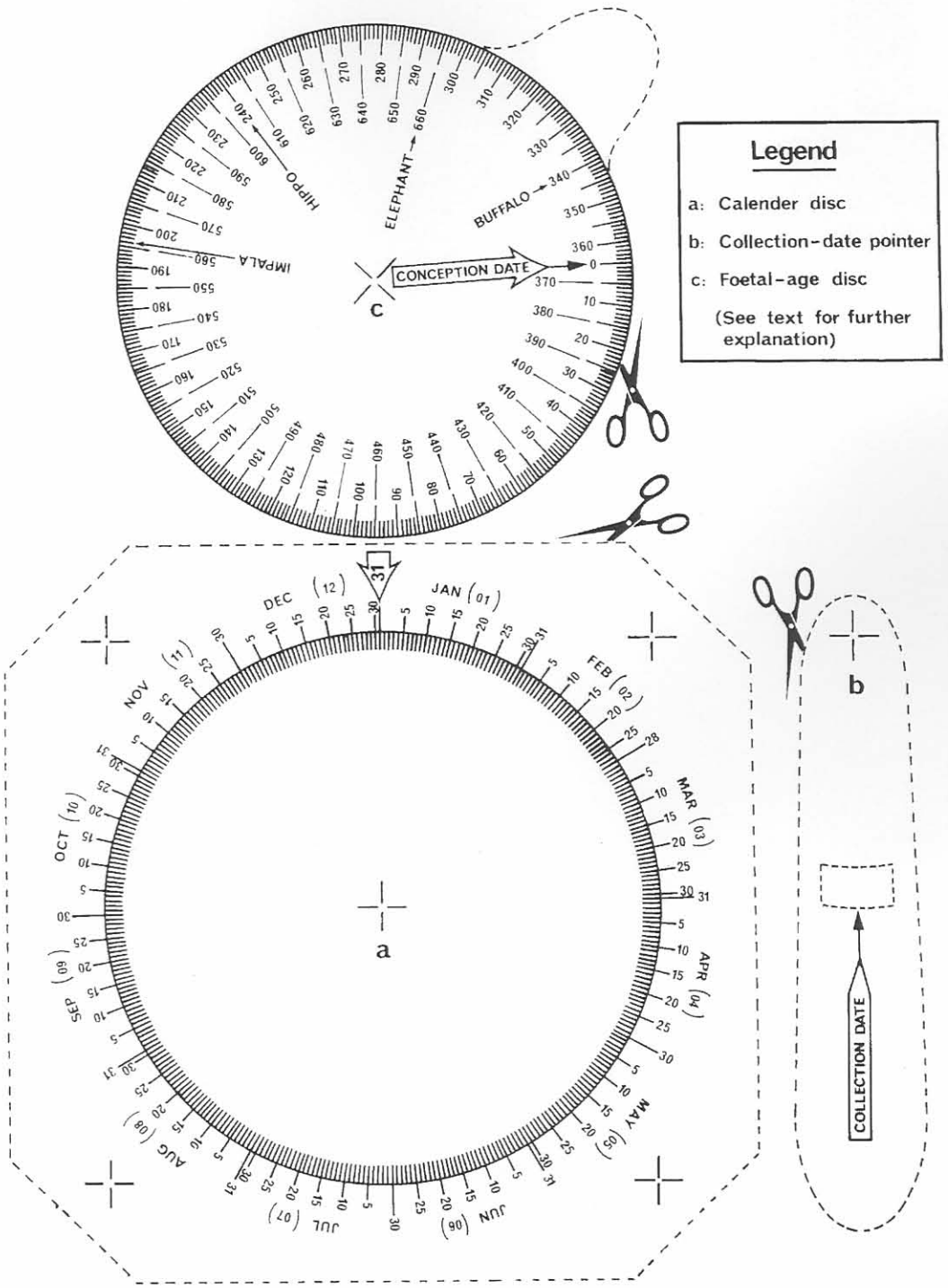


Figure 27: The three components of the device for the determination of foetal conception and birth dates from its conception age as determined by the Huggett and Widdas (1951) formula.