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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KNP and elephant management policies are derived from a literature survey which included books, scientific literature, unpublished reports, annual reports from KNP, and diaries of earlier Wardens and Rangers.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.

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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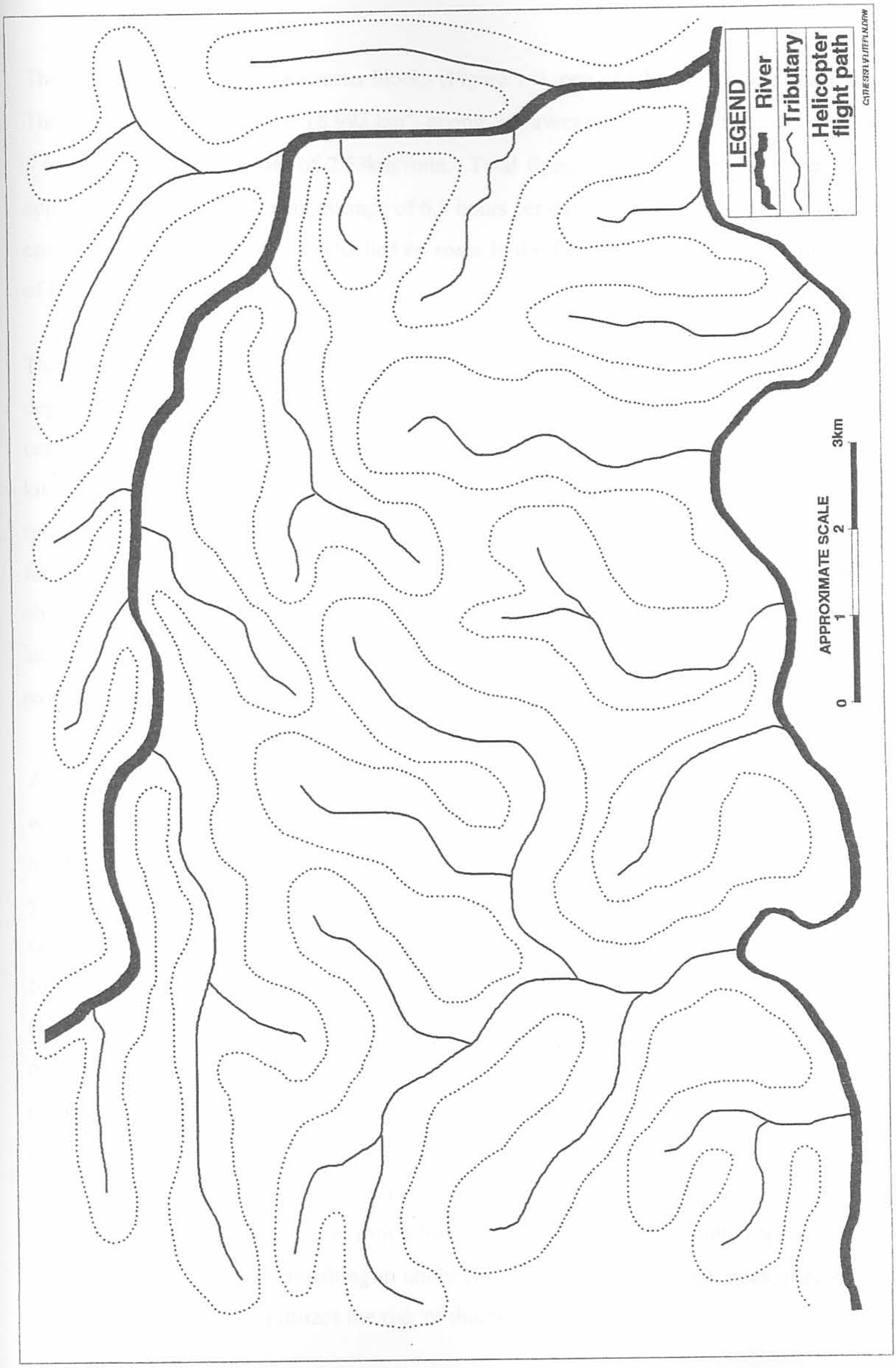

Figure 13: A graphic representation of the helicopter's flight path during aerial censuses of the elephant and buffalo populations of the Kruger National Park.

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.

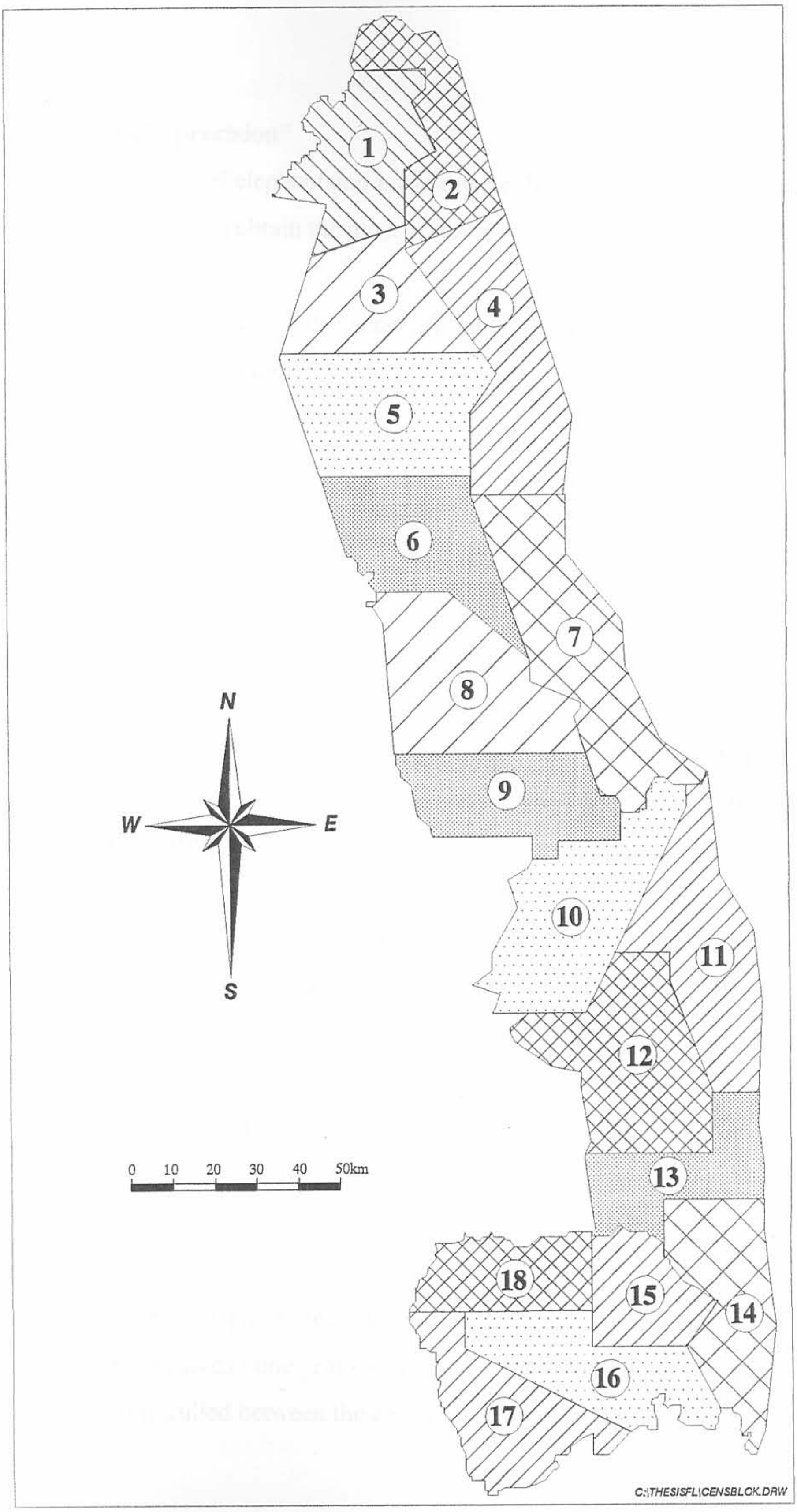

Figure 14: Aerial census compartments for the 18 days required to cover the total area of the Kruger National Park during annual censuses in August and September each year.

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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:

$$Ny+1 = Ny + By - Cy$$

where:

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

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

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

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[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.

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 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 $\boldsymbol{Year_{t+1} - Year_t}$ 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:

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

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:

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

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

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

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.

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.

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 $\overline{r}$. 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 $\overline{r}$ 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 $\overline{r}$ 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.

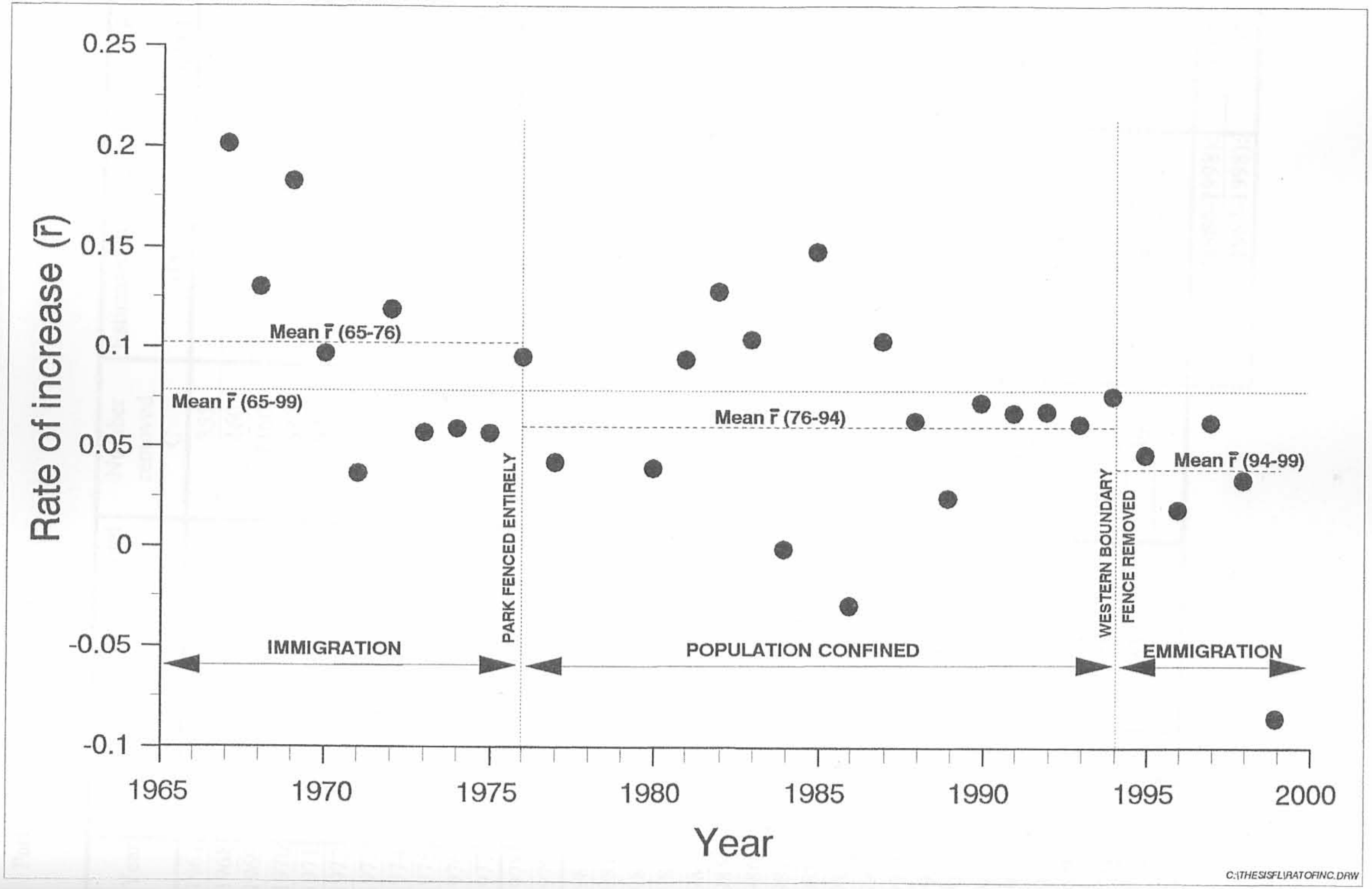

Figure 15: Rates of increase (r̄) of the Kruger National Park elephant population for respective years between 1967 and 1999.

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 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:

$$\mathbf{N}y\mathbf{+1 = N}y\mathbf{ + B}y\mathbf{ - D}y\mathbf{ - C}y$$

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[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 ($\overline{r}$) 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)	$\overline{r}$ 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.

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.

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.

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[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.

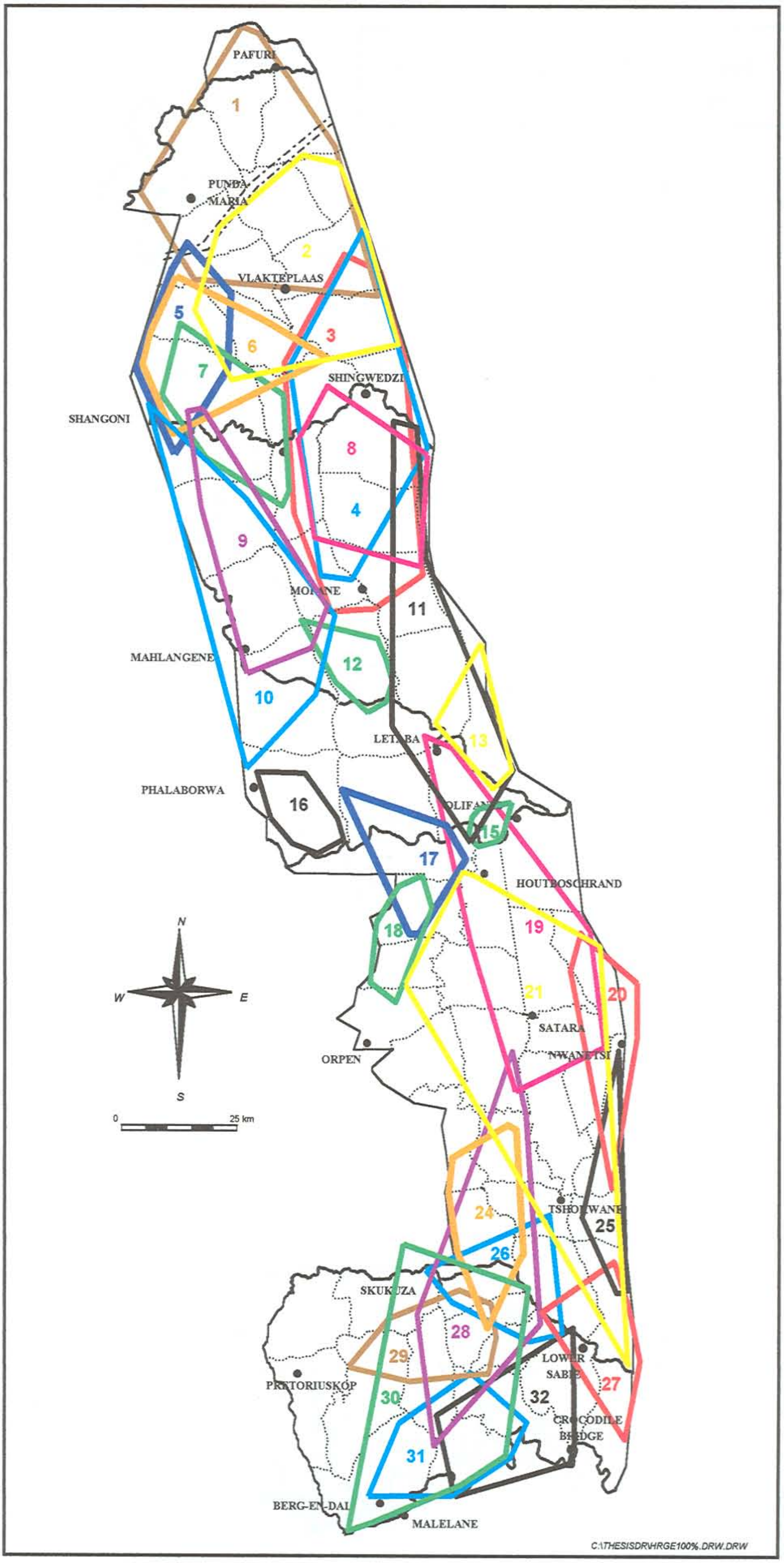

Figure 16: Minimum convex polygons (100% MCPs) showing the home ranges of 29 radio collared elephant cows in the Kruger National Park.

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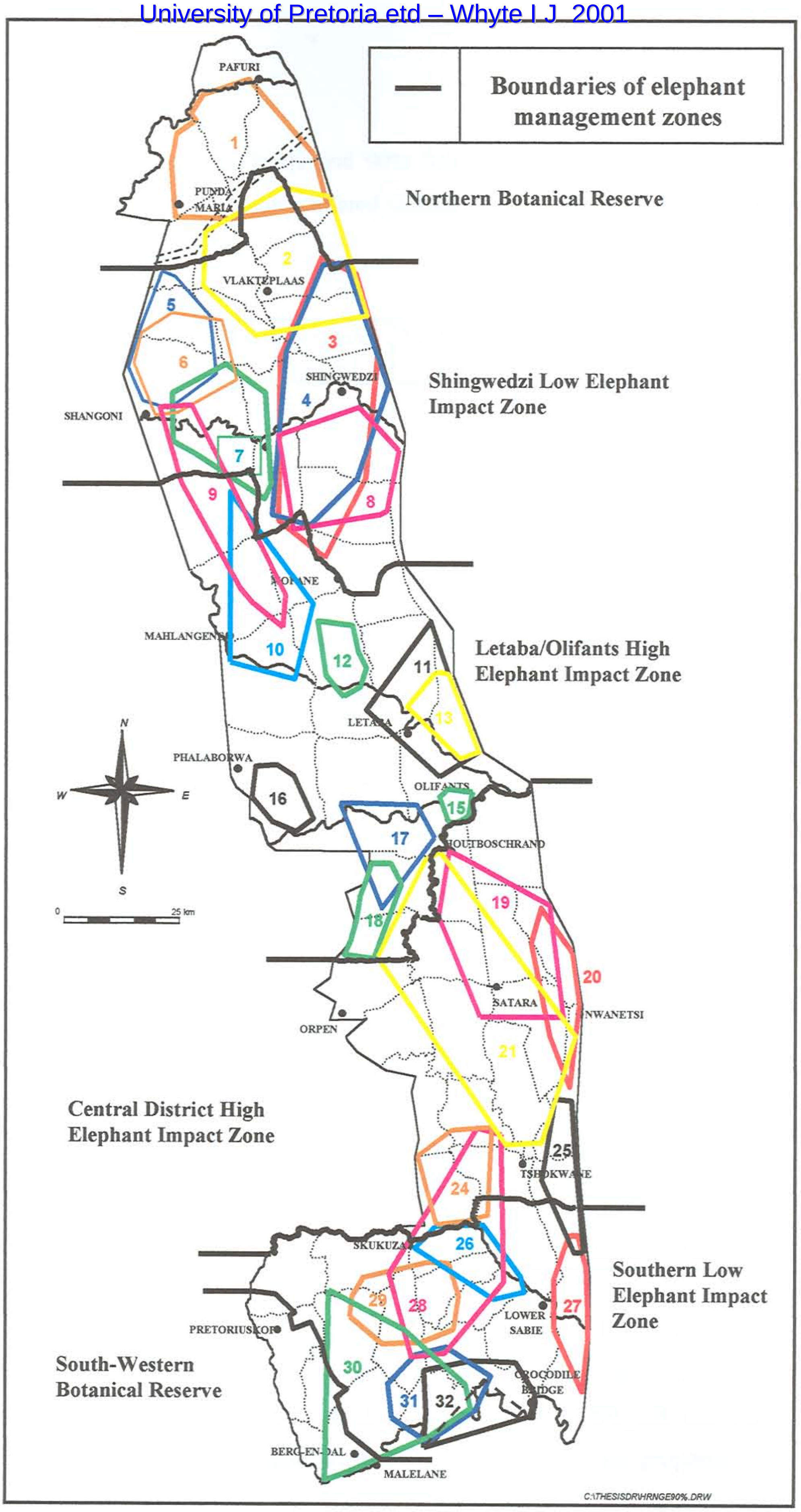

Figure 17: 90% MCPs of the home ranges of 29 radio collared elephant cows in KNP. Note how the boundaries of elephant management zones were defined on these home ranges.

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 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.

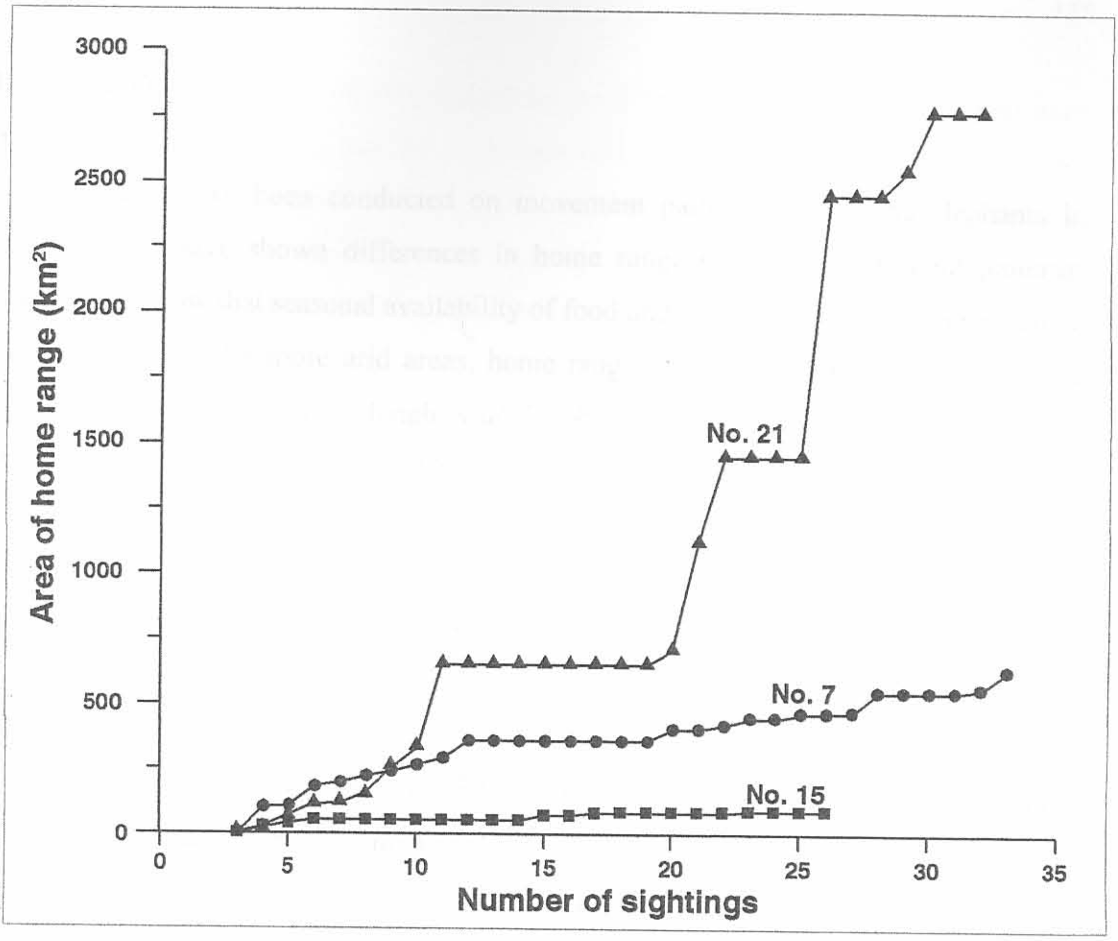

Figure 18: The relationship between the number of telemetry fixes and home range area of three selected radio-collared elephant cows in Kruger National Park (100% MCP's).

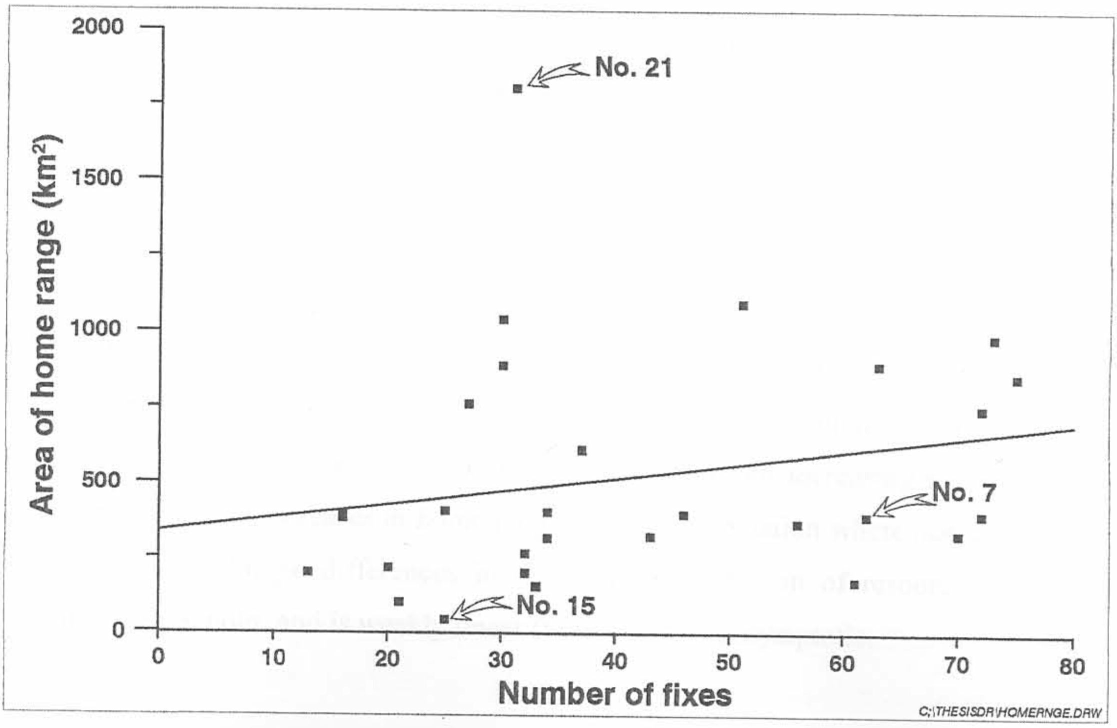

Figure 19: The relationship between the number of telemetry fixes and area of respective home ranges of radio-collared elephant cows in Kruger National Park (90% MCP's).

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.

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 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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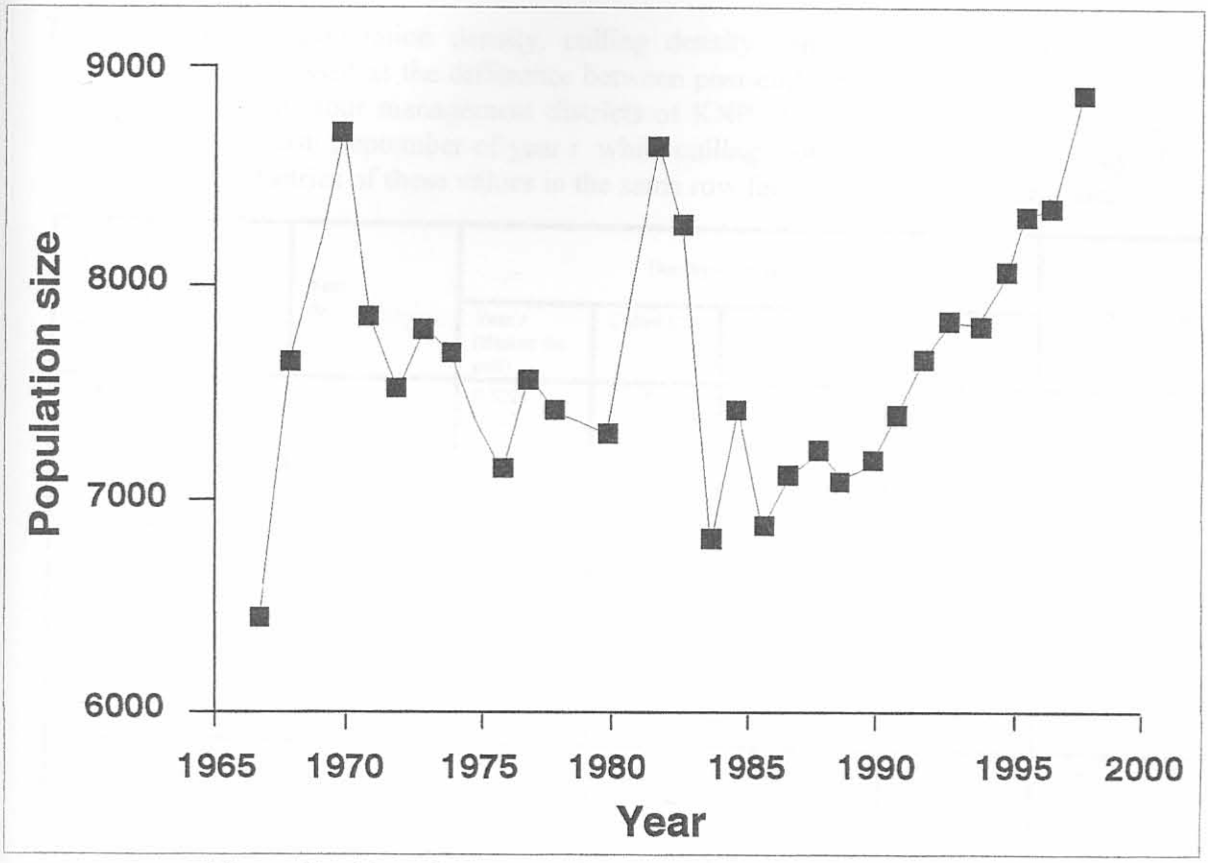

Figure 20: Trend in the total population size for African elephants in the KNP based on aerial surveys conducted annually between 1967 and 1998. The population was exposed to culling as a management option from 1967 to 1994.

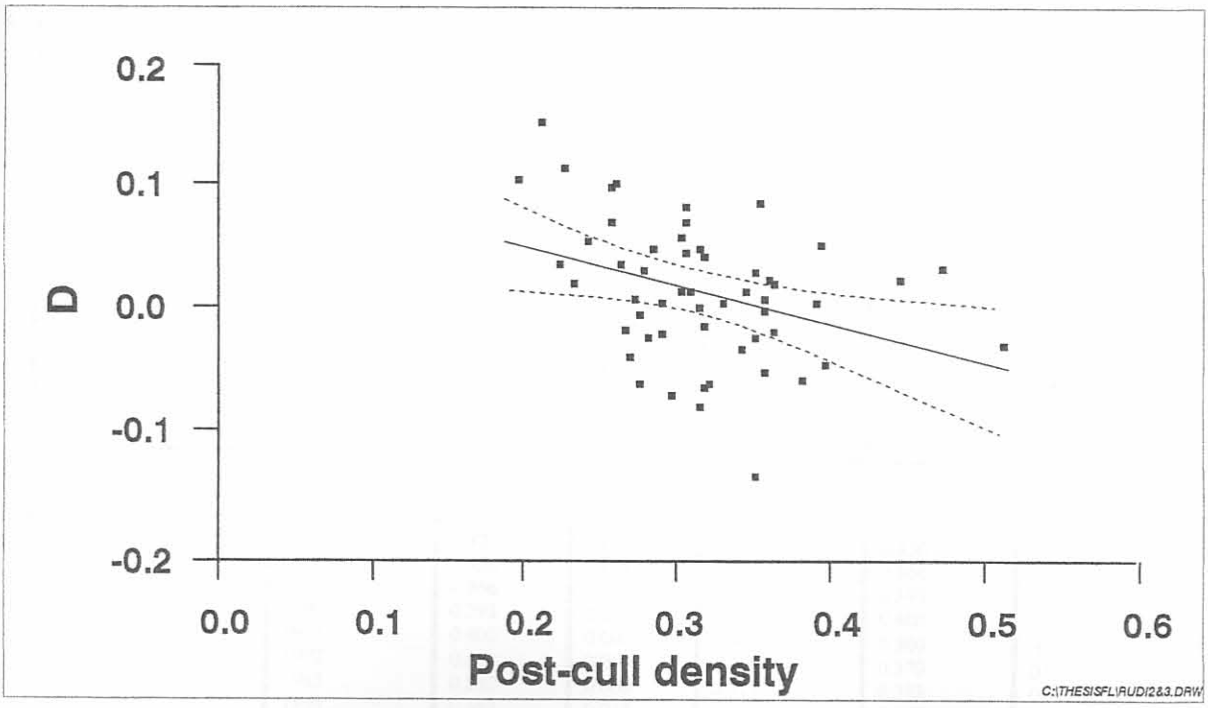

Figure 21: The relationship between change in population density (D) and post-cull density for all sub-populations of African elephants in the KNP.

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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		

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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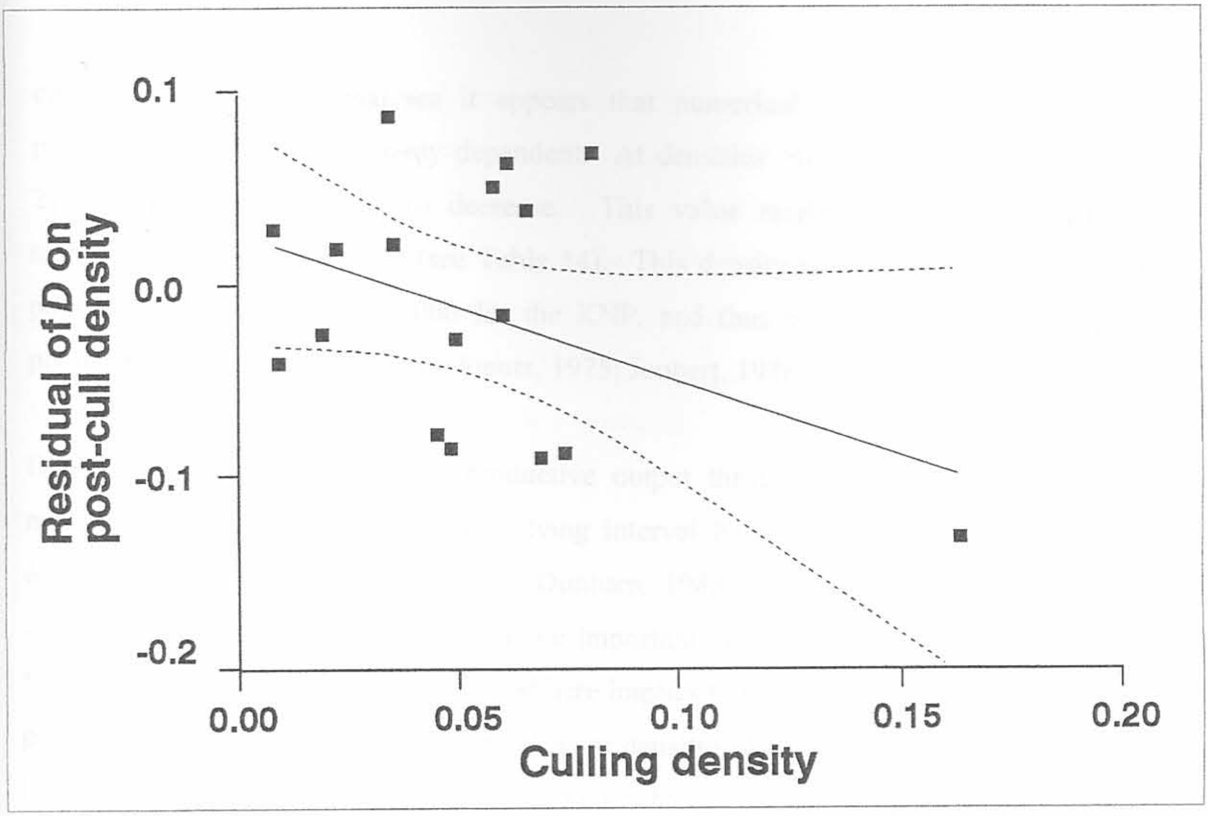

Figure 22: The relationship between the residuals of *D* on post-cull density and culling density described by a linear regression line with the equation $y = 0.0357 - 0.759x$ $(r = 0.173)$.

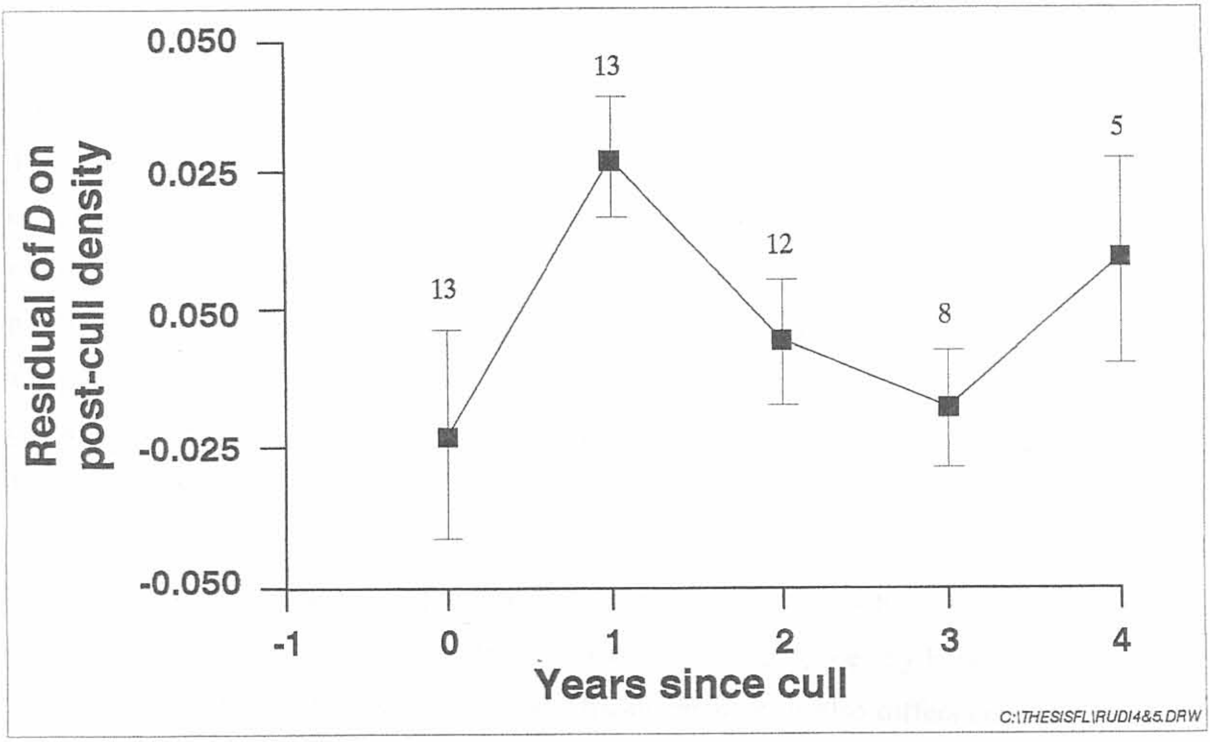

Figure 23: The influence of culling on population change expressed as the mean values of *D* on post-cull density against the number of years that have elapsed since culling. The above the standard error bars denote sample size.

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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 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

(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.