The ecology of the desert-dwelling elephants <u>Loxodonta africana</u> (Blumenbach, 1797) of western Damaraland and Kaokoland.

by

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ABSTRACT

The distribution, population biology, spatial organization, movements and habitat utilization of the desert-dwelling elephants residing in the northern Namib Desert region of the Kaokoveld, South West Africa are discussed. These elephants were present in the desert long before the advent of western man and the elephants' present distribution and **movements** indicate that they were and still are permanently and voluntarily in the

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The distribution, population biology, spatial organization, movements and habitat utilization of the desert-dwelling elephants residing in the northern Namib Desert region of the Kaokoveld, South West Africa are discussed. These elephants were present in the desert long before the advent of western man and the elephants' present distribution and movements indicate that they were and still are permanently and voluntarily in the

desert. No migration to or from the Etosha National Park took place during the study period. The elephants' social organization, social structure, sex ratio, age structure, age at sexual maturity, movements and feeding patterns correspond largely with that of other elephant populations in Africa and there is no indication that the desert environment has an adverse effect on the vitality or condition of the population concerned. Mortality, caused by illegal hunting, was decidedly the major population limiting factor and the cause of the decline in numbers up to 1982. Since 1982 the population stabilized and it is predicted that the population will double by 1997 in the absence of human induced mortality. The elephants' mobility, intimate knowledge of resource distribution within their home ranges and ability to go for extended periods without drinking water are regarded as key factors for their survival in the desert. The present number of elephants has no detrimental affect on the desert vegetation. These elephants fit well into, and probably provide a vital link in the desert ecology. The desert-dwelling elephants of the northern Namib Desert represent an unique ecotype of <u>Loxodonta africana</u>.

DEDICATED TO MY WIFE MARIANNE

AND MY THREE DAUGHTERS LYNETTE, MADELI AND ANNEMIE

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CHAPTER 1

INTRODUCTION

The western Kaokoveld, an area with breathtaking scenic beauty and an endless variety of habitat types, animal and plant life, represents an unique ecosystem unlike any other to be found in southern Africa. Apart from numerous endemic plants, insects reptiles, birds and mammals (Tinley 1971), the region is further endowed with floral contributions of both Angola and the central Namib Desert (Giess 1968). In addition, the presence of large mammals, usually more characteristic of higher rainfall regimes, such as the elephant Loxodonta africana, black rhinoceros Diceros bicornis, giraffe Giraffa camelopardalis, kudu Tragelaphus strepsiceros and the lion Panthera leo also contribute to the uniqueness of the western Kaokoveld Desert. The inhospitable coastline, notorious for its numerous shipwrecks, and the arid, rugged nature of the interior mountains ensure that the western Kaokoveld remained relatively untouched and unexplored until fairly recently.

Since the first western man entered the Kaokoveld it was renowned for its vast game populations. Thus it has often been described as the game reservoir of South West Africa (Andersson 1861, Von Moltke 1945, Bigalke 1958). The declaration of this area as a game conservation area (to be known with the Etosha National Park as Game Reserve number two) in 1907 ensured that this status quo was upheld until 1964. The Kaokoveld was then deproclaimed as a game reserve to create a homeland for the native people (Odendaal 1964). Today the Kaokoveld is characterized by an alarming rate of habitat deterioration and a reduction in game numbers. The introduction of veterinary services and artificial waterholes increased the numbers of the local livestock to a point where the carrying capacity of the region (Loxton, Hunting and Associates 1974a and b) was far exceeded, culminating in a massive livestock die-off in 1981 (Hofmann 1981, Jacobie 1982). The increasing competition for available habitat between livestock and game, more than illegal hunting, has caused the rapid decline of game in the eastern areas. Most of the game left are now restricted to the uninhabited western parts of the Kaokoveld, with only remnants of the earlier game populations scattered over the cattle ranges in the east.

This predicament again emphasized the need for a viable management plan for the region, not only from a conservation point of view, but also as a means for the long-term utilization of the natural resources. Therefore, in 1975, a study (Viljoen 1980) was initiated to gather basic ecological information for the Kaokoland. This information was used in the formulation of a master plan by Eloff, Bothma, Theron and Van Riet (1977) for the management, conservation and utilization of the natural resources in the Kaokoveld. One of the first assignments of Viljoen's (1980) study was to determine possible game migration routes between the Etosha National Park and the western desert regions of the Kaokoveld. It soon became evident that only the

Hartmann's mountain zebra Equus zebra hartmannae migrated to any extent between the Etosha National Park and the western desert regions. Elephant movements in and out of the Etosha National Park were confined to the eastern Kaokoveld in agreement with the observations of Owen-Smith (1970) and De Villiers (1981). It appeared that the desert-dwelling elephants, black rhinoceroses and giraffes are permanently confined to the desert region. This was contrary to expectations and justified a closer look at these animals which survive in an environment that is totally atypical of that in which these animals are usually found. By implication, these animals must also be adapted to the desert. If nothing else, they therefore probably represent unique ecotypes which may be irreplaceable upon extinction.

From these facts emerged the priority of conserving these animals in their "natural environment". The combination of animal and environment justifies their conservation not only from a scientific, aesthetic or ecological point of view, but also from an economic point of view as they will have an unsurpassed tourist potential, creating a sustained income in a region otherwise economically relatively unexploitable.

Obviously, the first essential step in the conservation of these animals and their environment is the declaration of a nature reserve which can be effectively controlled and managed. This has been proposed by Owen-Smith (1970), Tinley (1971), Joubert (1972), Page (1976) and Eloff et al. (1977). However, in spite of all these proposals, by 1979 no nature reserve or effective conservation measures ha~~ve~~d been implemented in the Kaokoveld, nor did it seem likely to happen in the near future. But time was running out, with the numbers of these animals declining at a alarming rate (Viljoen 1980).

The next essential step therefore was a research programme to study the animals involved in order to understand their limiting factors and ecological requirements which will aid in their conservation. Mistakes could not be afforded and the extinction of the desert-dwelling elephants, black rhinoceroses and giraffes was an unthinkable yet real possibility.

The present study was therefore directed at obtaining relevant data to aid in formulating management and conservation strategies with which to ensure the survival of the desert-dwelling animal populations, to establish whether they indeed represent separate ecological populations and what adaptational phenomena they exhibit to occupy that particular niche. From a practical point of view the active research was concentrated on the desert-dwelling elephant population, not because they were regarded as more important or glamorous than the other animals in the desert, but, by virtue of their size, they would have the greatest impact on the desert environment. Most of the earlier information (Shortridge 1934, Bigalke 1958, Tinley 1971) on these elephants were based on conclusions drawn from short visits to the region in question and these conclusions suffer from a lack of an intimate knowledge of the area, a lack which could be ascribed to the vastness of the territory and the inaccessibility of vast tracts of the Kaokoveld. An attempt was made in the present study to overcome the previous deficiencies by doing an in depth and on-site study of the desert-dwelling elephants over a period of three years.

At the onset of the present study, the Kaokoveld stood on the brink of an era of unprecedented change: With the advent of four-wheel-drive vehicles and the withdrawal of permit requirements for entering the region in 1978, people could then range over the region at will. It was also the intermediate period between handing over jurisdiction from the then Department of Bantu Administration and Development to the Department of Agriculture and Nature Conservation with the result that law enforcement was practically non-existent. The war in the region also caused an influx of fire-arms and lack of conservation control. Consequently illegal hunting was rampant. Matters were further degraded by the dramatic increase in ivory and rhinoceros horn prices (Jackson 1982). In addition it was in the midst of one of the worst droughts in human memory with a massive die-off of both wildlife and livestock.

The present study then also assumed a secondary but important role. The mere presence of the researcher as well as other conservation-minded people served as a deterrent to would-be poachers. Information gathered during the course of this study helped with the tracing of poachers and also made the general public aware of the situation in the Kaokoveld, resulting in the involvement of various institutions and increased law enforcement in the Kaokoveld. It was also instrumental in the termination of uncontrolled elephant trophy hunting in the region. In this way the study also made a secondary contribution towards the survival of the desert-dwelling elephants during a critical time period.

In summary then, the current study is aimed at:-

1. Obtaining relevant information on various aspects of the ecology of the desert-dwelling elephants in an attempt to define limiting factors operating on the population, especially as an aid to formulate management and conservation strategies with which to ensure their survival.

2. To make a contribution towards the understanding of the relationship between the ecology and adaptational phenomena of the desert-dwelling elephants.

CHAPTER 2

STUDY AREA

LOCATION

The study was done in the Kaokoland, Damaraland and Skeleton Coast Park regions of South West Africa. These areas are situated in the north-western corner of S.W.A (Fig. 1) between 11° 45′ and 14° 35′ E and 17° 00′ and 22° 40′ S. Before the recommendations of the Odendaal Commission (Odendaal 1964), the entire region was known as the Kaokoveld (Shortridge 1934, Vedder 1937, Wellington 1967). Most of the earlier descriptions and studies refer to the entire Kaokoveld and made no distinction between the Skeleton Coast Park, Damaraland or Kaokoland. The boundaries between these areas are purely political and have no ecological significance at all. Therefore, to simplify matters, the entire region between the Kunene and Ugab Rivers will from hereon be referred to as the Kaokoveld, bearing in mind then that Kaokoland refers only to that portion of the Kaokoveld north of the Hoanib River (Figs. 1 and 2).

For the main purpose of studying the desert-dwelling elephants, the majority of observations were confined to an area west of the 150 mm (Fig. 3) isohyet in Damaraland and Kaokoland and north of the Ugab River, including the whole of the Skeleton Coast Park. Covering approximately 4,5 million ha, this latter area, because of certain geomorphological and vegetation characteristics, is known as the northern Namib Desert (Wellington 1967, Giess 1968)

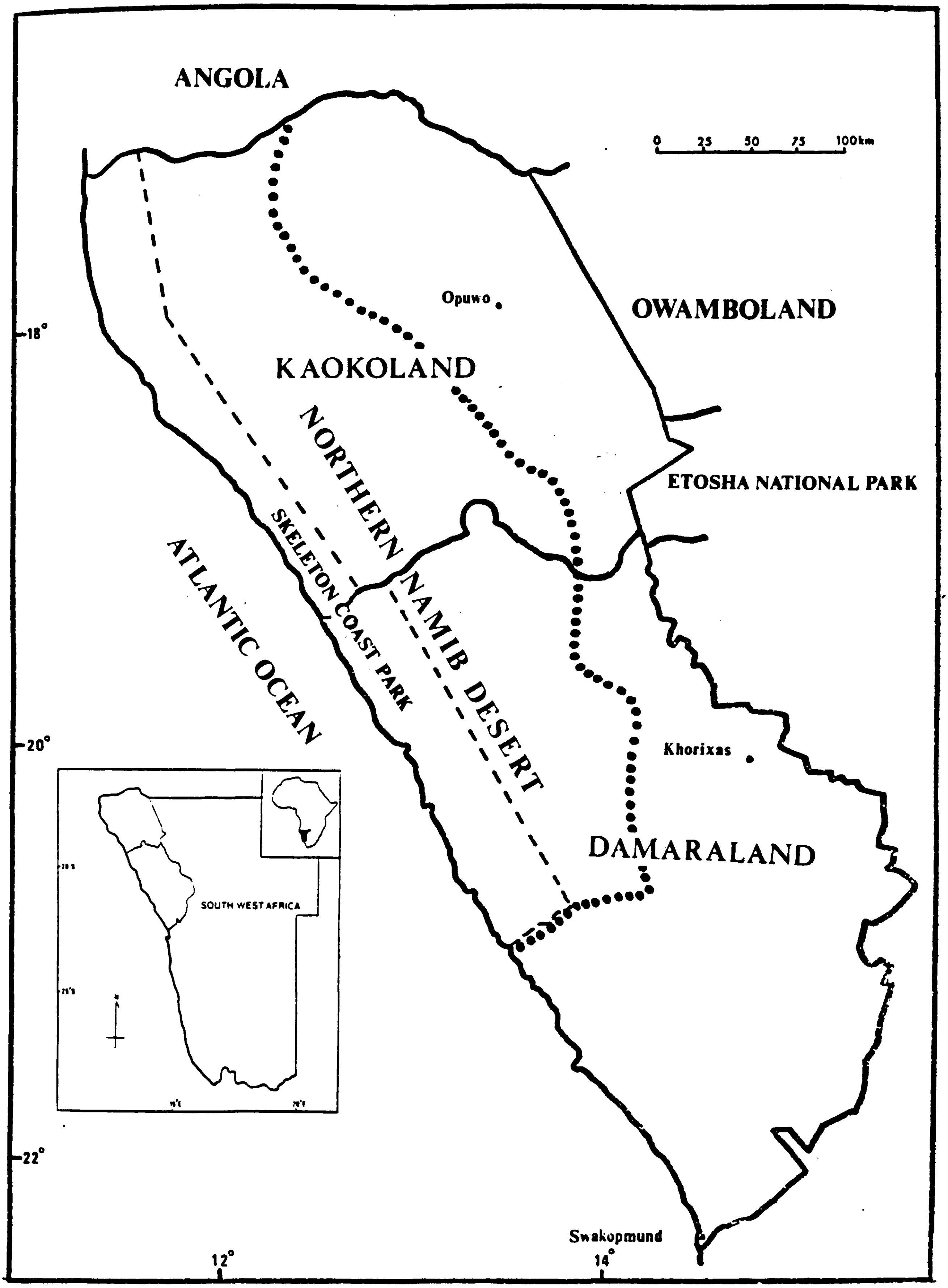


Figure 1: Location map of the study area, showing the locality of the Kaokoveld and the approximate extent (dotted line) of the northern Namib Desert.

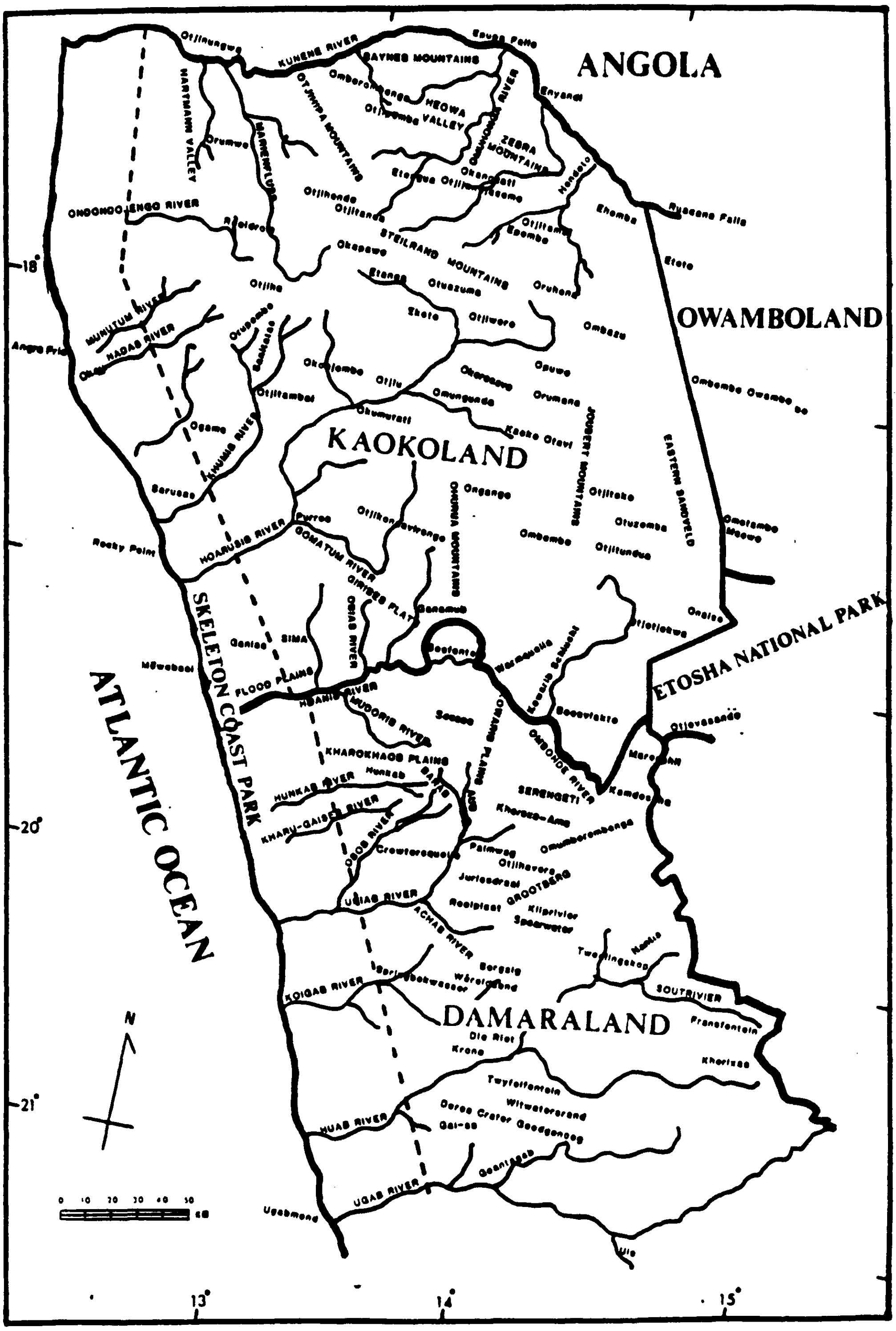


Figure 2: Map of the Kaokoveld, South West Africa, showing the locations mentioned in the text.

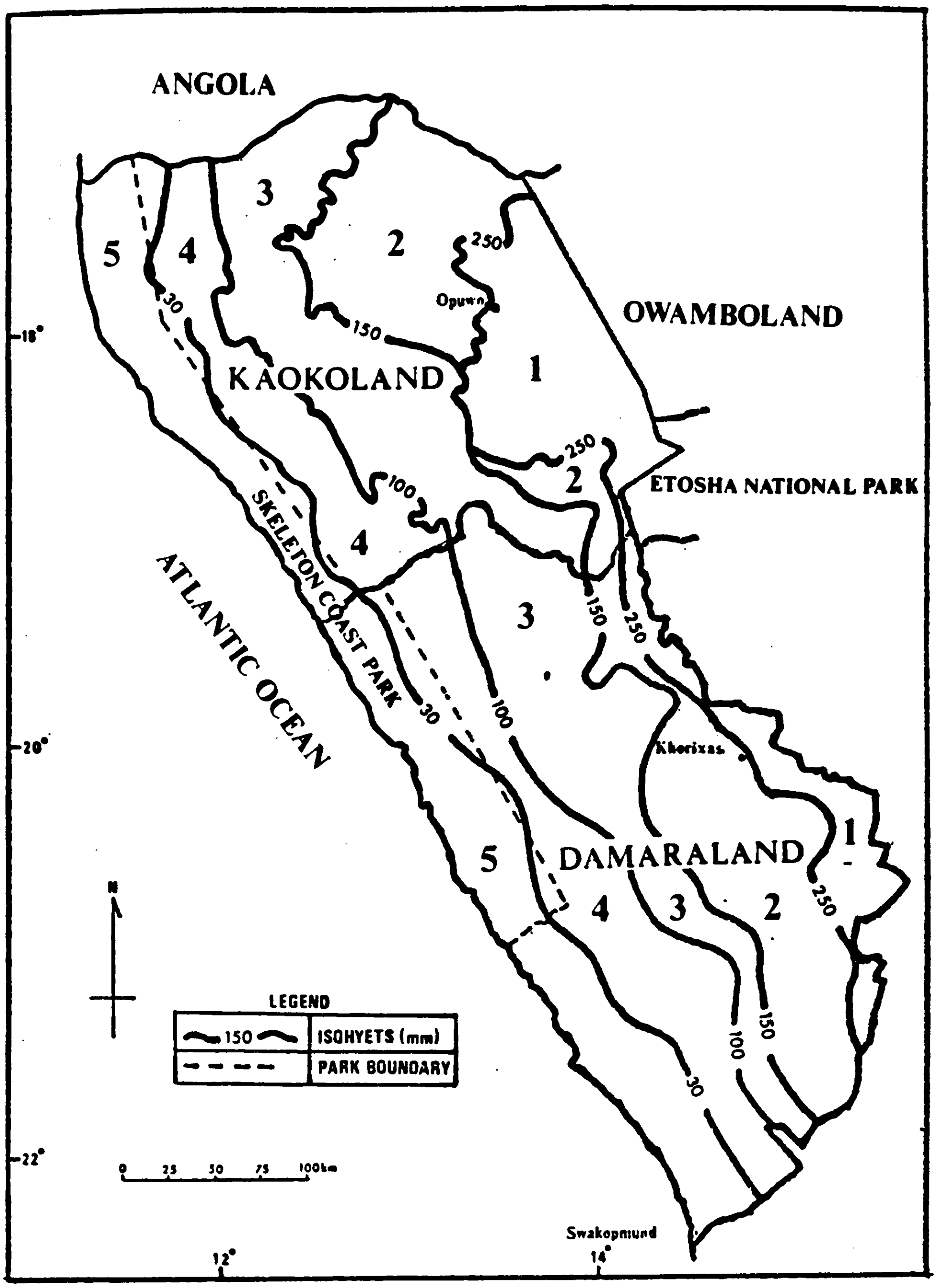


Figure 3: Mean annual isohyets and bioclimatic regions in the Kaokoveld, South West Africa, based on the division by Loxton *et al.* (1974a and b).

Bioclimatic regions:

1. Eastern Highland Plateau. 251 - 350 mm rainfall per year.
2. Central Drainage Basin. 151 - 250 mm rainfall.
3. Escarpment Zone. 101 - 150 mm rainfall.
4. Inner Namib Zone. 31 -100 mm rainfall.
5. Coastal Desert Zone. 0 - 30 mm rainfall.

and will hereafter be referred to as such. The northern Namib Desert is bounded in the north by the Kunene River, the west by the Atlantic Ocean, the south by the Ugab River and in the east by the arbitrary 150 mm isohyet. The 150 mm isohyet roughly follows a line from the Otjihipa Mountains in the north to Sesfontein in the south; thence it follows the contours of the Grootberg south to Uis (Fig. 2).

DESCRIPTION OF THE STUDY AREA.

TOPOGRAPHY

Some eleven million hectares in extent, the largest portion of the Kaokoveld can be described as mountainous broken by undulating plains. In the west, the bare mountain ridges are surrounded by sandy, gravel or stony plains. Dry river courses traverse the region from east to west and act as carriers of water and vegetation from the higher rainfall areas. The highest peak in the Baynes Mountains is 2 039 m above sea-level but the mean height of the Kaokoveld above sea-level is between 600 and 1200 m. The rainfall varies between 350 mm per annum in the east to less than 30 mm in the west, the main feature being the erratic and sporadic localized rain, resulting in long droughts and short flood periods. The Kaokoveld is divided into five bioclimatic regions (Fig.3) based on the divisions by Loxton, Hunting and Associates (1974a and b) in conjunction with the available rainfall figures and vegetation. The area is also rich in natural water-holes which supply a wide spectrum but low concentration of animal species (Viljoen 1980).

The main administrative centres are Opuwo (Ohopoho), Khorixas and Sesfontein and together with a few other locations such as Okangwati, Terrace Bay, Orumana and Aus are the only villages with some sort of infrastructure. There are only five major all-weather roads, traversable by two-wheel-drive vehicles. The rest of the region can only be negotiated by four-wheel-drive vehicles, often without the benefit of any type of road. A veterinary game fence which starts south of the Uniab River mouth in the west and continues up to the Etosha National Park in the east, cuts through the study area. Otherwise the territory is unfenced and offers unrestricted movement for game.

Of ecological importance is the 150 mm isohyet (Fig. 3) which, although not clearly defined, serves as an effective barrier between the different land-use forms in the Kaokoveld. To the east of the 150 mm isohyet some 30 000 local people practise a mainly migratory livestock production and among them they own in the region of 200 000 head of cattle and another 250 000 of small stock (Division of Veterinary Services, S.W.A. Unpublished Report). To the west of the 150 mm isohyet the area is only sporadically utilized by cattle and other livestock and today it serves as a sanctuary for those species of wild animals which are adapted to survive in desert conditions.

GEOMORPHOLOGY

Based on information provided by Wellington (1967) four main physiographic regions can be distinguished in South West Africa, and all four are represented in the Kaokoveld, namely:

The western Namib Region.

Between the escarpment region and the Atlantic coast the Namib surface rises to an altitude of 900 m at the foot of the escarpment mountains with an average width of about 130 km. The western Namib Region can be subdivided into two zones namely, the seaward zone, known as the coastal desert and the second zone, the inner Namib which is distinguished from the coastal zone by a steeper gradient, increasing vegetation, a more rocky and stony surface and by the absence of dunes.

In the western Namib region the coastal desert narrows in places to less than 16 km, widening elsewhere to about 60 km as in the vicinity of the lower Kunene River. Immediately to the east of the coastal flats the land surface does not rise smoothly as it does further south, but does so steeply and ruggedly with numerous bare ridges of Archaean granite - gneiss and schist, or of the hard Kaoko Lava which rises at Orupembe to a height of 1 200 m. The main lava mass, however, is found in the southern part of the Kaokoveld, between 19° 30′ and 21° 00′ S where the lava covers an area of about 10 000 km^2, extending from the coast to the escarpment edge. The uppermost flow, of hard rhyolite here, has protected the lower softer bands from rapid weathering and erosion, so that the lava surface rises in places to great heights of which the Grootberg is an example.

The Escarpment Region.

The dividing line between the northern Namib Desert region and the Plateau Hardveld Region is the plateau edge or great escarpment. In the northern Kaokoveld, the Otavi Beds, dipping towards the Etosha Basin, strike north, the limestone quartzite forming a good medium for scarp formation. The Kunene, Hoarusib, Khumib and Hoanib Rivers cut back into these beds through deep, narrow gorges leaving the plateau edges fairly definite but dissecting the plateau surface behind the escarpment, resulting in a complex mountainous region. In the Otjihipa Mountains the escarpment reaches it's most scenic grandeur where the Kunene River leaves it's lower gorge through the Baynes Mountains to enter the northern Namib Desert Region. Here the escarpment attains a height of about 2 000 m above sea level, towering above the Marienfluss sand plains and the Hartmann Mountains to the west. The escarpment continues northwards into Angola. In southern Kaokoveld in the Otavi Beds of the Damara System, there is no clear trace of a plateau edge. The most common ridge-like features there are the interfluves between the larger stream beds where granite, marble and quartzite frequently form rugged hills and ridges.

The Flateau Hardveld Region.

Between the great escarpment and the sandveld lies the Plateau Hardveld Region which extends from the Kunene River in the north to the Orange River in the south. The northern part of the region is known as the Damara Region of which the Otavi Highlands are represented in the Kaokoveld. The Otavi Highlands are formed of Damara Beds of which the hard quartzites and limestones are strongly folded, forming high ridges. With the limestone are associated the usual karstic features: lack of surface water and the occurrence of eyes or springs. In the Kaokoveld Region, strong springs occur in limestone beds at Kaoko Otavi, Otjijanjasemo and several other localities. In the north-western part of the plateau (Tjimba Highlands), the folded Otavi Quartzites rise to 2 039 m above sea level in the Baynes Mountains which form the southern wall of the Kunene Gorge. Other high elevations manifest as the Joubert and Otjihipa Mountains. The ruggedness of this area is so marked that large parts of the area are still inaccessible as is nearly the whole Escarpment Region. Unlike the Kalahari Sandveld Region, the Plateau Hardveld Region has a high run-off after rain, and the sandy river-beds of this region, even in the dry season, generally contain fairly large supplies of subsurface water at shallow depths.

The Kalahari Sandveld Region.

This is an extension of the great Kalahari Basin, which reaches across the Owamboland Plains westward to be represented in the east of the Kaokoveld. The Kalahari Sandveld Region is built up of secondary lime deposits covered by a layer of aeolian sand of varying depths, mostly red or yellow brown in colour. In the vicinity of Omotambo Maowe, where there is deeper sand, stable dune ridges are present. The drainage in the Kalahari Sandveld Region is undefined and consists of a number of shallow, indistinct ditches draining into shallow pans. Otherwise the region is unfeatured.

Loxton et al. (1974a and b) differentiate between 32 physiographic regions in the Kaokoveld. Similarly, the geology of the region is discussed in detail by Martin (1965), Loxton et al.(1974a and b), Malan and Owen-Smith (1974) and Miller and Schalk (1980). Some of these details, where applicable, will be related to later in the present study.

VEGETATION

The vegetation of the Kaokoveld ranges from a *Colophospermum mopane* Savanna in the east to a sparsely vegetated desert in the west, with only isolated and arid-adapted plants, mainly restricted to the watercourses in the latter. Giess (1971) described the vegetation of the Kaokoveld broadly as a *Colophospermum mopane* Savanna and a northern Namib Desert. Other descriptions of the vegetation, such as those of Owen-Smith (1970), Malan and Owen-Smith (1974) and Loxton et al. (1974a and b) were mainly based on physiographic and topographic boundaries.

For the Kaokoland region, north of the Hoanib River, Viljoen (1980) recognised 14 veld types with the dry river courses as a 15th veld type. Here the eastern veld types consist of a maximum density of 2085 trees and shrubs per hectare, but which rapidly decrease towards the west to less than one shrub per hectare. The herbaceous layer consists mainly of a temporary covering of annual grasses during the short rainy season. Most of the veld types recognised by Viljoen (1980) for Kaokoland can be extended into Damaraland . The vegetation of Damaraland is described by Loxton _et al._ (1974b) and De Sousa Correira (1976) although they lack some detail because no quantitative plant surveys have yet been done in Damaraland. Where applicable, the various vegetation types will be discussed in more detail later on in this study.

HABITAT TYPES

The term 'habitat' has been used in a variety of ways. Mostly it simply is the place where an organism lives (Smith 1966; Moore 1968; Odum 1971; Kritzinger, Labuschagne and Pienaar 1972; and Abercrombie, Hickman and Johnson 1973). In another sense, however, it is interchangeable with the word 'biotype', meaning a particular community. For example, certain biotypes have been described as 'woodland habitat' or 'savanna habitat' (Krebs and Davies 1978, Evans 1979). In general it is difficult to find two authors using exactly the same definition of the word 'habitat'.

Habitats may also be described with different degrees of precision depending on the organism being studied. For example in insect studies the term 'micro-habitat' may be used to cover the finer distribution of an insect which may be restricted to a particular part of a particular plant. The larger the organism gets, the broader is the description of its habitat. For example, an antelope's habitat is often described as woodland or as grassland, which may encompass a large variety of plant communities, soils, climate or geography. Similarly, a large mammal such as an elephant may utilize a number of different habitat types during a single day in terms of a smaller animal's life requirements.

In the broadest sense then the habitat of the desert-dwelling elephants can be described as the northern Namib Desert, this being nearly the smallest viable unit for these elephants' survival. However, as the present study is concerned with the elephants' area and food selection, vegetation utilization, ecological influence and seasonal movements, habitat types were delineated according to areas with a homogeneous vegetation. For this the term forage habitat is preferred here because it has that significance to the larger mammals (Kutilek 1979). For the purpose of this study then the term forage habitat is defined as a region with a homogeneous geomorphology and vegetation physiognomy.

For the purpose of the present study, the following forage habitat types are recognised in the Kaokoveld. The habitat types are divided into two categories, namely the higher rainfall habitat types in the east receiving 150 mm or more rain per year and the lower rainfall desert habitat types in the west receiving less than 150 mm of rain per year.

A. Habitat types receiving less than 150 mm of rainfall per year in the Kaokoveld.

1. The Coastal Desert.

This habitat consists of the sand dunes, rocky ridges and the sand or gravel plains of the coastal desert. The mean annual rainfall is less than 30 mm and the temperatures are low with a mean daily temperature of 16,2°C. Coastal fog is a common occurrence. The main characteristic is the scarce and widely scattered vegetation (Viljoen 1980). The permanent vegetation here is represented by low-growing shrubs less than 400 mm high. Trees are totally absent. For the greater part of the year this habitat is deficient in terms of the ecological requirements of most larger animals. However, when it does rain, the annual grasses provide a high quality but low quantity food, apparently preferred by the species of larger game.

2. The Gravel Plains.

This habitat is the transitional zone between the Coastal Desert and the Escarpment Mountains and extends over the length of the Kaokoveld. It consists of flat to undulating plains covered with gravel up to 30 mm in diameter. Estimated annual rainfall is between 30 and 80 mm per year. The coastal fog frequently extends into this habitat type, but with the absence of the coastal winds, temperatures are generally much higher than at the coast. The vegetation is mainly ephemeral but perennial shrubs are present in the shallow water courses. Like the coastal desert habitat, this habitat is also for a large part of the year unfit for the species of larger game, although there is a concentration of game on the plains during the rainy season when Stipagrostis spp. grasses are available.

The Rocky Plains.

The flat to undulating plains, covered with rocks up to 300 mm in diameter is characteristic of this habitat. Rocky plains extend over the length of the Kaokoveld connecting the mountains and ridges mostly to the west of the escarpment range. In the central areas this habitat extends eastwards as far as the Grootberg Mountain range. The estimated annual rainfall is between 80 and 120 mm. Trees are confined to the shallow water courses but shrubs may be abundant in the eastern ranges of the rocky plains. The ephemeral grass cover is low even in years with a high rainfall. The vegetation is similar to that of the mountains habitat and can also be regarded as an important dry season habitat for browsers.

The Sandy Plains.

This habitat is represented by wide, deep, sandy plains enclosed by high, steepsided mountains. The presence of circular patches devoid of vegetation on these sandy plains is a striking characteristic of this habitat. Between 400 and 600 m above sea level the estimated yearly rainfall is between 100 and 120 mm. Trees are absent or widely scattered but this is the only habitat type west of the 150 mm isohyet with perennial grasses. In areas with good grass cover the sandy plains habitat can be utilized by game throughout the year.

The Mountains.

The mountains and ridges of the escarpment and adjacent areas enclose this habitat type. The extremely rocky disposition and steep slopes are characteristic of this area. The estimated annual rainfall is from 100 to 140 mm. Trees are sparse but shrubs, mainly Commiphora spp., reach a density of up to 346 plants per hectare in some areas. The grass cover is mainly ephemeral but as a result of the large variety of shrubs the mountains are an important dry season habitat for the larger animals.

The River Courses.

With the exception of the Kunene River, all other rivers in the Kaokoveld are seasonal. These seasonal rivers act as lifelines for the desert in being able to drain rainwater and to support vegetation from the higher rainfall areas to the east. The mesophytic vegetation of most rivers is in sharp contrast to that of the rest of the surrounding environment. This is the only habitat in the west of the Kaokoveld which supports large trees and a dense shrub cover. The grass cover is mainly ephemeral but with a large number of trees and shrubs present, this is one of the most important dry season habitats. Also, with rain generally falling earlier in the season in the east, as compared to the west, and with the resultant flooding of the western rivers, this is the first habitat type which has a herbaceous growth at the start of the rainy season. In most rivers, water can also be obtained throughout the year by digging in the sandy riverbeds. This highlights the importance of this habitat for game during the dry season.

The Flood Plains.

Most seasonal rivers in the Kaokoveld are blocked off from the sea by sand dunes. East of these dunes small alluvial plains develop where water accumulates during river floods, resulting in an abundance of low-growing shrubs. The vegetation of the flood plains are maintained by water from river floods which originate in the higher rainfall eastern regions, resulting in a higher primary production and a richer food source than would normally occur under the prevailing rainfall regime. After river floods this habitat type provides an important source of green vegetation in the absence of rain in the surrounding areas.

Habitat types east of the 150 mm isohyet in the Kaokoveld.

The Tree and Shrub Savanna.

Covering the largest area in the eastern Kaokoveld, this habitat consists of wide, undulating to broken valleys and plains, covered with relatively dense stands of trees and shrubs. Different plant communities resort under this habitat type, but in the context of this study all areas with the same plant physiognomy and geomorphology are regarded as the same forage habitat as far as the life requirements of the larger animals are concerned. Most of the trees and shrubs are deciduous and with a few exceptions all the grasses and herbs are annual. This habitat type is also utilized by a large number of domestic animals which compete with the game for the available food and water.

The Open Savannas.

The open savannas consist of level valleys or plains in which the trees grow more than three times their canopy diameter apart and where shrubs are virtually absent. In areas which are not overgrazed, perennial grasses are conspicuous and have a relative basal cover of 7,4 per cent. Otherwise the open savannas are trampled to a fine powdery dust. This habitat is also utilized by a large number of domestic animals.

The Eastern Sandveld.

An extension of the great Kalahari Sandveld Region, this habitat consists of undulating, sandy plains with permanently vegetated dunes in some areas. The vegetation is mainly a tree or shrub savanna with predominantly perennial grasses. As a result of the absence of surface water this habitat is mainly utilized by game species.

The Eastern Mountains.

All the mountains and ridges in the eastern Kaokoveld are included in this habitat type. Reaching an altitude of more than 2 000 m above sea level, the main characteristics are the shallow soil and steep slopes. This habitat type ranges from an open savanna to thick stands of dry forests in ravines and other protected areas, with the herbaceous layer predominantly annual. The plant species composition is heterogeneous, but the basic geomorphology and physiognomy remain the same. In some areas, this habitat type is heavily utilized by domestic stock.

The Eastern Rivers.

The vegetation of the seasonal eastern rivers is characterized by large trees and dense stands of trees and shrubs on the banks. The herbaceous layer is virtually absent as a result of overgrazing by domestic stock. This habitat type does not play such an important role in the survival of the game species as in the west because of the higher rainfall and the greater plant biomass in the adjacent habitat types.

CLIMATE.

GENERAL

Relatively little information is available on the climatic conditions prevailing in the Kaokoveld and no long-term data exist. Only seven meteorological stations exist within the territory and there are large areas for which no records are available. Consequently, and for the sake of continuity, some of the climatic data given here are based on data recorded in adjacent areas. Climatological data for the appropriate meteorological stations are derived from unpublished information of the Pretoria and Windhoek Weather Bureaux.

The climate of the Kaokoveld is mainly controlled by the movements of the South Atlantic Anticyclone, the cold Benguela Current and the upwelling of cold waters, under the influence of off-shore south-east trade winds on the west coast (Schulze 1965). Another important factor is the location of the northern Namib Desert which lies mainly in the rainshadow below the escarpment mountains and is dependent on rains of which the moisture is taken up by north and north-west winds of the warm Agulhas Current on the east coast of Africa. By the time that these winds reach the Kaokoveld escarpment mountains after a westerly movement over thousands of kilometres, they are mostly devoid of moisture.

Barnard (1965) distinguished three climatic zones in the Kaokoveld, namely:

The cool coastal desert.

This region includes the coastal zone up to 30 km inland. The climate is dominated by the upwelling of cold waters from the Benguela Current with the result that the temperature is 6-7 °C lower than what is normal for this latitude. Large-scale condensation and precipitation cannot take place as a result of the dense, cool air. This is also the reason why rain is practically non-existent in this region. The relative air humidity is high (mean : > 80 per cent) and advective fog is virtually a daily occurrence. The temperature is moderate during all seasons and the daily and seasonal fluctuations in temperature are slight. As a result of the oceanic influence there is a marked delay in the seasonal change of temperature. Characteristic is the incidence of south to south-westerly winds, especially in the summer months as a result of local atmospheric depressions during the day. In the early winter months the occurrence of berg winds from the east, which cause a temperature increase of 15 - 20 °C within hours, is also a characteristic of this climatic zone.

The warm Namib Desert.

This climatic zone is basically a transition between the coastal zone and plateau regions and shows characteristics common to both. The temperature is 4-5 °C higher than on the coast and shows only slight seasonal changes. The cool south-western sea-breeze during the summer months has a restraining effect, with the result that the summer temperatures are lower here than expected. During March and April, this latter effect is cancelled by warm east winds so that the highest temperatures are usually measured during these months. The rainfall is predominantly of a late summer convectional type, and the mean annual rainfall varies between 50 mm near the coast and 150 mm on the plateau side. The main feature of this area is the erratic and sporadic localised rains resulting in an annual variability of up to 100 per cent so that mean annual rainfall figures are nothing more than arithmetical means and have little other significance. Most of western Kaokoveld is within this climatic zone.

The transitional desert of eastern Kaokoveld.

The largest part of the eastern Kaokoveld is also part of the great plateau of South West Africa. The result is that climatic conditions there link up with that of Owamboland further to the east. As a whole it is typically subtropic: the winters are warm and temperate, and the summers hot with the maximum temperature occurring in early summer. Because of the high temperatures, the summer precipitation of 300 mm to 450 mm per annum is still too low to counter the rate of evaporation.

RAINFALL

According to Wellington (1967) and Malan and Owen-Smith (1974), the formation of a low-pressure zone over the Kalahari Desert attracts a stream of moist air from central Africa and the Indian Ocean to the Kalahari Desert in early summer. The cooling effect brought about by rain falling in the Kalahari Desert disperses this large low-pressure system, enabling the cloud-bearing air to be drawn westwards across the continent by a series of minor low-pressure areas. By the time that this air reaches the Kaokoveld much of the moisture has been lost after traversing vast tracts of high ground.

Rainfall occurs in summer and the highest precipitation can be expected from January to March, but significant falls may occur from November to April. During the remaining six months little or no rain falls. As mentioned earlier, the most significant feature of the rainfall in the Kaokoveld is the extreme variability and its unreliable, sporadic nature. For example at Sesfontein the annual rainfall was 77,0 mm in 1980, nothing in 1981, and 149,4 mm in 1982, while up to 98 per cent of the annual rain can fall in one month. The Coefficient of Variation in annual rainfall for Sesfontein is 93,25 per cent (n=10). This results in long and frequent droughts and short flood periods.

A further feature of the rainfall in the Kaokoveld is the marked reduction in rainfall from east to west (Table 1). The rainfall isohyets tend to run parallel to the coast, but show considerable deviation due to topography. In the extreme east the annual rainfall is more than 300 mm, decreasing to less than 30 mm on the coast in a distance of less than 250 km. This reduction is mainly caused by a variation in velocity between the dry western winds and the moist east winds. There is also a difference in the month of maximum rainfall between east and west. In the west the maximum rainfall is approximately two months later than in the east. The mean monthly rainfall figures for the relevant weather stations appear in Table 1.

On the basis of isohyets Loxton _et al._(1974a and b) distinguished four bioclimatic zones for the Kaokoland region and three for the Damaraland region. They made no distinction between the Coastal Desert and Inner Namib Zone and also used different isohyets in Damaraland and Kaokoland to define the bioclimatic zones. However, from Barnard (1965) and according to Viljoen (1980) five distinct bioclimatic zones can be discerned in the Kaokoveld. Therefore, the designation of the different zones by Loxton _et al_.(1974a and b) was revised in this study to be more descriptive and to be representative of the whole Kaokoveld (Fig. 3). The isohyet lines depicted in Figure 3 do not represent distinct borders between bioclimatic zones since the transition between the different zones are gradual. However, there is a conspicuous difference in vegetation composition and physiognomy midway between the isohyet lines.

Table 1 : Mean monthly and mean yearly rainfall (mm) recorded at weather stations in and around the Kaokoveld, South West Africa (Weather Bureau, Dept. of Environmental Affairs, Pretoria).

WEATHER STATION AND BIOCLIMATIC ZONE: EAST TO WEST	ALTITUDE IN METRES	OBSERVATION PERIOD	MONTH												YEAR
			J	F	M	A	M	J	J	A	S	O	N	D	
Eastern Highland Plateau															
Opuwo	1155	1939-1974	90,5	67,8	86,2	24,9	0,9	0,0	0,0	0,0	1,7	12,7	31,5	36,4	352,6
Otjovasandu	1050	1968-1985	66,3	74,5	67,1	26,9	1,2	1,6	0,0	0,0	0,1	5,8	19,2	24,3	287,0
Kamanjab	1200	1968-1985	50,7	72,8	75,8	12,4	0,8	4,1	0,0	0,0	0,0	14,7	15,6	11,1	258,0
Central Drainage Basin															
Khorixas	900	1968-1985	44,9	55,7	68,3	25,3	0,4	0,3	0,0	0,0	0,3	0,0	8,0	10,2	213,4
Uis	784	1966-1979	42,1	45,3	61,3	10,0	0,7	0,0	0,0	0,0	0,9	0,1	6,1	8,9	174,5
Escarpment Zone															
Sesfontein	577	1902-1975	19,0	23,5	32,5	11,9	3,2	0,2	0,0	0,1	0,2	1,8	6,0	9,7	108,1
Inner Namib Zone															
Springbokwasser	500	1981-1985	1,7	3,6	28,4	12,5	0,0	0,3	0,0	0,0	0,0	0,0	0,0	0,4	54,4
Coastal Desert															
Möwebaai	16	1968-1985	2,9	2,9	12,0	0,2	0,0	0,6	0,1	0,1	0,0	0,0	0,2	0,0	19,0
Ugabmond	20	1978-1985	1,6	3,4	10,2	1,9	0,1	3,1	0,0	0,2	0,0	0,0	0,0	1,6	20,4

TEMPERATURE

The atmospheric temperature in the Kaokoveld, like that elsewhere, is coupled to the latitude, the height above sea level and the prevailing wind systems. Temperature records in the Kaokoveld are available from only three stations and no long term data are available. In general, the temperature can be regarded as moderate, but there are indications of extremely high temperatures (up to 40 °C in the shade on a local thermometer) in the summer months in the Kunene Valley. During the winter months the temperature is relatively high, but the absence of *Colophospermum mopane* in some eastern valleys indicates the presence of frost (Loxton *et al.* 1974a).

The mean monthly temperatures for weather stations in the Kaokoveld appear in Table 2. The mean summer temperatures in the east range from 34,2 °C to 18,8 °C , while in the winter they vary between 26,6 °C and 5,7 °C. The temperatures in the Escarpment Zone tend to be the same as in the east although the winter temperatures are more moderate (Table 2). Along the coast there is a smaller fluctuation in temperature, but it is also cooler than inland. For example, the variation in maximum temperature for winter and summer at Möwebaai is between 11,0 and 21,8 °C.

PREVAILING WINDS

The development of an early summer low pressure-zone over the Kalahari Desert draws a stream of mainly westerly and south-

TABLE 2: Mean monthly maximum, minimum and daily temperatures (°C) recorded at weather stations in the Kaokoveld, South West Africa (Weather Bureau, Dept. of Environmental Affairs, Pretoria).

WEATHER STATION	ALTITUDE IN METRES	OBSERVATION PERIOD	MONTH												YEAR
			J	F	M	A	M	J	J	A	S	O	N	D	
<u>Opuwo</u>	1155	1968-1974													
maximum			32,6	31,5	30,5	30,5	28,8	26,6	27,2	28,7	32,6	34,2	33,8	34,1	
minimum			16,2	15,4	17,1	14,4	8,7	6,1	5,7	7,1	9,8	13,8	15,0	14,9	
daily			24,4	23,4	23,8	22,4	18,7	16,4	16,3	17,9	21,2	24,0	24,4	24,5	21,5
<u>Uis</u>	784	1966-1979													
maximum			32,5	33,0	33,6	32,5	29,6	27,4	27,6	29,0	31,0	31,9	33,1	32,4	
minimum			16,5	17,6	19,0	16,5	12,6	10,6	9,9	9,8	11,2	13,5	15,6	15,2	
daily			24,5	25,3	26,3	24,5	21,1	18,8	18,7	19,4	21,1	22,7	23,3	23,8	22,5
<u>Möwebaai</u>	16	1968-1975													
maximum			20,7	21,2	20,9	19,7	18,6	19,0	17,9	15,9	16,4	17,2	18,3	19,4	
minimum			16,2	17,0	16,4	15,2	12,8	11,6	11,2	11,0	12,3	13,2	14,2	14,9	
daily			18,5	19,1	18,7	17,5	15,7	15,3	14,6	13,5	14,4	15,2	16,3	17,2	16,3

westerly winds through the Kaokoveld, winds which flow towards the Kalahari low. Later in the summer this low disperses, causing an inclination for the air to move westwards again, bringing easterly and north-easterly winds to the Kaokoveld in the process. With these winds the long awaited rains usually falls. During winter months, dry easterly winds, derived from anticyclones off the east coast, dominate most of South West Africa (Wellington 1967).

The coastal lowlands are little affected by the interior circulation of air and here strong south to south-westerly winds blow almost unceasingly throughout the year. Exceptions are occasional northerly winds during the summer and hot berg winds in the winter.

SEASONS

From the available climatological data and from personal observations, it is clear that there are basically only two seasons in the Kaokoveld, namely the wet or rainy season and the dry season. Ecologically, however, the dry season can be subdivided into a cold dry season and a hot dry season. The minimum and maximum mean daily temperature changes during the winter months (cold dry season) are moderate (6 - 8 °C), and there is still food and water for herbivores, stimulated by the rains of the previous season, available. However, from September onwards, during the hot dry season, most of the food plants of herbivores are either dead or have been utilized completely and many of the water-holes have dried up. This period also corresponds with the hottest months of the year and it is during this season with limited available water and food that a herbivore's adaptation is taxed to the utmost.

Therefore, on the basis of the combined ecological and climatological data, three seasons rather than two are distinguished in the Kaokoveld, namely the wet season, the cold dry season and the hot dry season (Viljoen 1980). The demarcation of the seasons as schematically represented in Figure 4 therefore are based on a combination of the mean monthly rainfall, mean monthly temperature and other ecological considerations. The month of May is included in the wet season as the influence of the rains in April is still predominant in May, through the abundance of food and rainwater pools. Also, although the rains in the eastern Kaokoveld normally start to fall in October, November or December, the precipitation is still much lower than the evaporation with the result that the first rains have little or no influence on the vegetation or general ecology of the eastern Kaokoveld. These months are therefore still regarded as part of the hot dry season.

The wet season is, however, also delayed from east to west in the Kaokoveld as the western region receives it's optimum rainfall approximately two months later than the eastern Kaokoveld (Table 1 and Fig. 4). For this reason, the wet season in the northern Namib Desert region is demarcated from March to May as the low

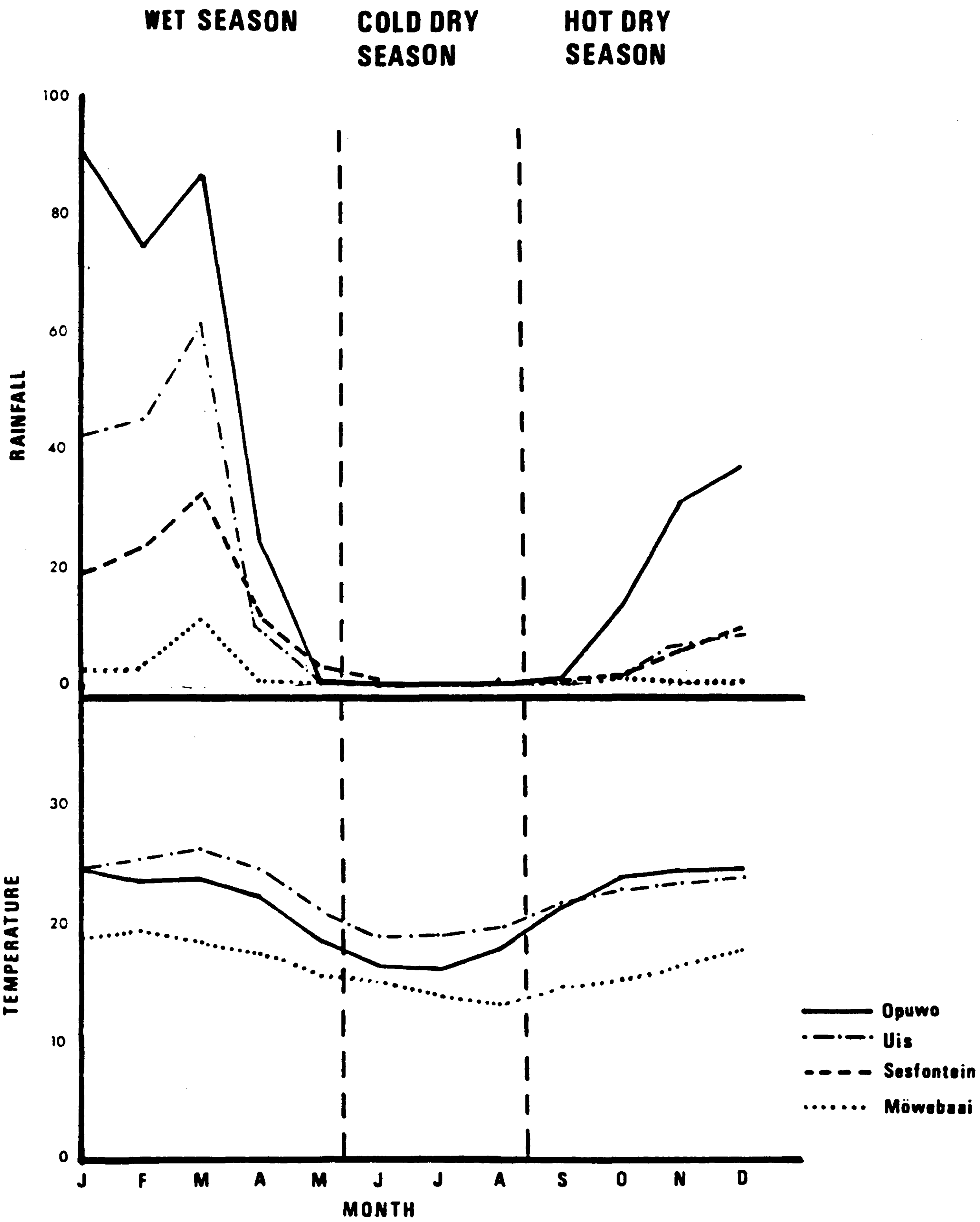


Figure 4: Graphic representation of the mean monthly rainfall (mm) and mean monthly temperatures (°C) recorded at weather stations in the Kaokoveld, illustrating the demarcation of the three ecological seasons (see text).

rainfall before March has little influence on the vegetation or general ecology of the western regions.

ENVIRONMENTAL CONDITIONS DURING THE PERIOD OF STUDY.

As one of the aims of this study was to determine the influence of rainfall and environmental conditions on the movements and distribution of the desert-dwelling elephants, a brief account of the rainfall pattern in the northern Namib Desert region of the Kaokoveld between 1977 and 1983 is presented in Table 3.

Although Möwebaai had a higher annual rainfall in 1978 and 1979 than the long-term mean for Möwebaai, the rest of the region, as manifested by the Sesfontein rainfall figures, averaged between 31 and 100 per cent below the annual long-term mean precipitation (Table 3). This low rainfall resulted in severe drought conditions which lasted from 1977 up to 1981. At the end of this five-year drought, virtually the whole study area was denuded of grass and herbs while most deciduous shrubs remained leafless. Many water-holes, previously thought off as permanent also dried up. The magnitude of the drought is well illustrated by the fact that more than 80 per cent of the population of large mammals in the Kaokoveld died as a result of this drought (Viljoen 1982b). The exception was the elephants, giraffes and black rhinocerosses all being apparently little affected by the drought. The occurrence of river floods in 1980 and 1981, resulting from rain in the east probably prevented a complete

Table 3: Annual rainfall (mm) in the northern Namib Desert region of the Kaokoveld, South West Africa, between 1977 and 1983.

WEATHER STATION	LONG-TERM MEAN	RAINFALL							1977-1981 MEAN
		1977	1978	1979	1980	1981	1982	1983	
Sesfontein	108,1	33,5	73,0	63,0	77,0	0,0	149,8	88,3	49,3
Möwebaai	19,0	9,8	24,3	24,5	0,0	1,2	31,9	0,5	12,0

die-off of the larger mammals. These river courses together with the upper reaches of the Barab River which received an isolated rain shower in 1981, remained the only habitats with any sort of nourishment for the larger mammals during the five-year drought period.

The drought was finally broken in 1982 when the total annual rainfall at Sesfontein exceeded the long-term mean by 94 per cent. The widespread rains in 1982 resulted in a spectacular recovery of the desert vegetation, insect and bird life. Excessive floods during that year also caused the Hoanib River to break through the 10 km wide belt of dunes that previously blocked its course to the sea, resulting in an abundance of green plants and water-holes in the far west which lasted long into the hot dry season with a corresponding influence on the movements of the desert-dwelling elephants.

The information on elephant movements and distribution gathered during this study therefore covered all environmental conditions, representing both a period of extremely dry conditions and a period of environmental resource abundance.

CHAPTER 3

STATUS AND PAST AND PRESENT DISTRIBUTION OF ELEPHANTS IN THE KAOKOVELD, SOUTH WEST AFRICA.

INTRODUCTION

The study of the distribution of a species is often on integral part of the study of its ecology, and a knowledge of historical changes in distribution is a prerequisite for species conservation programmes. The concept of distribution, defined as the geographical occurrence of a species (Garmonsway 1979), is well understood by naturalists.

The usual and universally practised method of determining this distribution is by simple direct or indirect observation and plotting. While this method is widely employed and accepted, especially in short-term studies, it might in some studies lead to misleading information and interpretation. The reason for this is that some animals, such as elephants, have occasional infrequent movements far out of their normal range. These movements, which can best be described as exploratory movements or wanderings, might lead to gross misinterpretation of the elephant's habitat requirements or population trends if they were included into their distribution range. This is so especially when comparing the past and present expansion or reduction of the elephant's distribution. Known examples of the elephant's vagrant nature are the appearance of a lone elephant in the Mafikeng district in 1971, some 700 km from its normal distribution range (Skead 1980) and the movements over 600 km of an elephant herd from the Kaokoveld to the south of Otjivarongo and back again (Von Moltke 1945). During the present study it became clear that a detailed long-term knowledge of the range occupation and movements of the species in question was necessary to give an accurate and representative distribution pattern .

The determination of the past distribution and the status of a species is equally important in conservation. Such data can provide information on population trends, habitat selection, the origin of a population and its relationship with neighbouring conspecifics. Unfortunately, in trying to determine the past distribution of a species in a given area, one usually has to rely on incidental observations of travellers who had little knowledge of the area or the animal concerned at the time of their travels.

The present part of the study examines the past and present distribution and status of all the elephants in the Kaokoveld (Kaokoland, Damaraland and the Skeleton Coast Park). Emphasis is placed on the desert-dwelling elephants that occupy the northern Namib Desert region west of the 150 mm isohyet (Fig. 3) in the Kaokoveld. A primary aim of the initial study was to discover trends in population density and distribution of the desert-dwelling elephants, and to examine the hypothesis that the occupation of the northern Namib Desert by elephants is a recent phenomenon induced by human disturbance and pressure during the last 20 years (Schoeman 1982 and 1984). Secondarily, the aim was to provide information for an understanding of their habitat requirements, movements, dispersion and their relationships with other elephant populations.

METHODS

The data on the past distribution of the elephants in the Kaokoveld were based on published works, journals of travel, hunting, geological and historical reports, newspaper cuttings, rock engravings and place names. An attempt was made to study all published material of travellers to the region , but in most cases only incidental information of this nature was available.

Information on the recent distribution and status of the elephants was obtained during two study periods; the first of two-and-a-half years between 1975 and 1978 (Viljoen 1980) and the second of three years duration between 1980 and 1983. Data accumulation involving travelling some 130 000 km by vehicle, 370 hours of aerial surveys and uncounted kilometres on foot. Direct sightings of elephant provided data on numbers and distribution, whereas indirect observations (spoor, dung etc.) provided additional data on distribution. Seasonal movements were monitored on a monthly basis to provide an unbiased distribution pattern. The historical periods used here are more a reflection of available information than anything else.

RESULTS

DISTRIBUTION BEFORE 1800.

Vedder (1937) recounts an expedition in 1793 when a certain Van Reenen and Pienaar journeyed from Walvis Bay to the Swakop River mouth where they found "good water and also dense vegetation - together with many wild animals like elephant, rhinoceros, gemsbok and springbok." Pienaar then also journeyed 12 days upstream along the Swakop River and found an abundance of game, shooting three elephants and two rhinoceroses. While the Swakop River is well outside the present range of distribution of the desert-dwelling elephants, this record indicates that elephants were present in the Namib Desert before the advent of western man.

No other written records exist for this period, the main reason probably being that nobody with any literate knowledge was in the Kaokoveld before 1800. However, there are other indications of early elephant presence in the western regions. At Twyfelfontein and at Sossos south of Sesfontein, where there are numerous rock engravings, elephants feature prominently. While it might be argued that the artists could have moved a long distance after observing an animal before engraving it, it is conspicuous that with one doubtful exception (Vierech and Rudner 1957), only the animals that today still occur in the area, are featured there. The age of these engravings is unknown, but judging from the amount of oxygenation on the engravings it can be stated that they are very old (Vierech and Rudner 1957).

DISTRIBUTION AND STATUS BETWEEN 1800 AND 1900.

Information for this period is also scanty, but the few records that do exist show beyond doubt that elephants occurred in the Namib Desert. Alexander (1838), commenting on a journey to Walvis Bay in 1837, quotes the Namaquas as follows: "We are always afraid of meeting the Damaras on the seashore, to which they occasionally come on their hunting expeditions, after elephants and other large animals in the Swakop River". Alexander (1838) also reported that elephants were said to be numerous about the Swakop River and that the Bushmen in the Kuiseb River were exterminated by the Damara people, elephants and other wild animals. In March 1855, according to a newspaper report (In: Vedder 1937), an expedition was undertaken by the Governor of Mossamedes to the Kunene Mouth. They could travel only a short way (about 3 km) up the Kunene River because of the rocky terrain. The Governor reported that "Game, especially elephants were seen in great numbers". After that expedition many elephant hunting trips were undertaken to the Kunene Mouth.

In 1861 Andersson (1861) reported elephants at a waterhole in the Omaruru River. The first reliable record of elephants actually occurring in the northern Namib Desert, however, came from Hartmann (1897 and 1902) during his epic journeys through the

Kaokoveld. Hartmann reported seeing herds of elephant, giraffe, impala and rhinoceroses in the Marienfluss. Also on a journey from the Nadas Waterhole (Okau) to the Kunene River, they encountered many game, including elephants.

Most of the information on elephant distribution in eastern Kaokoveld before 1900 came from the Dorslandtrekkers who hunted elephants in that area from 1880 up to 1908 (Von Moltke 1945). Their hunting covered a large part of the Kaokoveld, of which they obtained a first-hand knowledge, and they were also the first who quoted elephant numbers. The accuracy of the numbers are, however, doubtful as the hunting area covered was much larger than the present day Kaokoveld, and was, in most cases, based on hearsay or on a memory span of 45 years (Von Moltke 1945). It was also probably a subjective overestimation as the Dorslandtrekkers had to justify the large numbers of elephants which they had killed because of public criticism. In the numbers and dates quoted, there are many conflicting statements. For example a certain D.J.Robbertse stated (In: Von Moltke 1945) that 2 000 elephants were hunted in the Kaokoveld between 1880 and 1908. At a later stage he mentioned that he only joined the hunting in 1894 and that they had shot between 50 and 182 (page 150) or 130 to 160 elephants (page 273) a year. From his description it was also clear that these figures include all the elephants that were shot in Angola and Owamboland. Robbertse remarked that they shot only bulls and that there must still be thousands of elephants left in the Kaokoveld (in 1945).

An interesting observation was made by F.Robbertse who apparently counted 3 000 elephants in 8 herds in a valley west of Okorosave. He is quoted by D.J.Robbertse 45 years later and confirmed by J.H.Robbertse (Von Moltke 1945). The number of elephants in that valley must have been an overestimate, as it is well-known how difficult it is to count even a herd of 30 elephants accurately in bush country. A personal visit by the present author to the valley in question also showed that it would be hard put to harbour 3 000 elephants, even if they were standing side by side. Whatever the case, the Dorslandtrekkers knew the Kaokoveld better than anybody else at that time and their locality descriptions are regarded as reliable even if the numbers of elephants seen and shot are questioned.

The elephant records reported for the Kaokoveld up to 1900 are summarised in Figure 5. It would appear that the elephants were widely distributed over the whole of eastern Kaokoveld and probably in the northern Namib Desert as well. How many elephants there actually were, will never be known, but the mere fact that the Dorslandtrekkers hunted there for 28 years with practically no restrictions indicate that there must have been a large viable population. Of the 2 000 elephants claimed to have been shot by the Dorslandtrekkers a large percentage could have been shot in the Kaokoveld. An original total population of between 2 500 and 3 500 elephants is estimated as a base to allow the above-mentioned hunting pressure. The estimation is based on the mean number of elephants shot per year (2 000

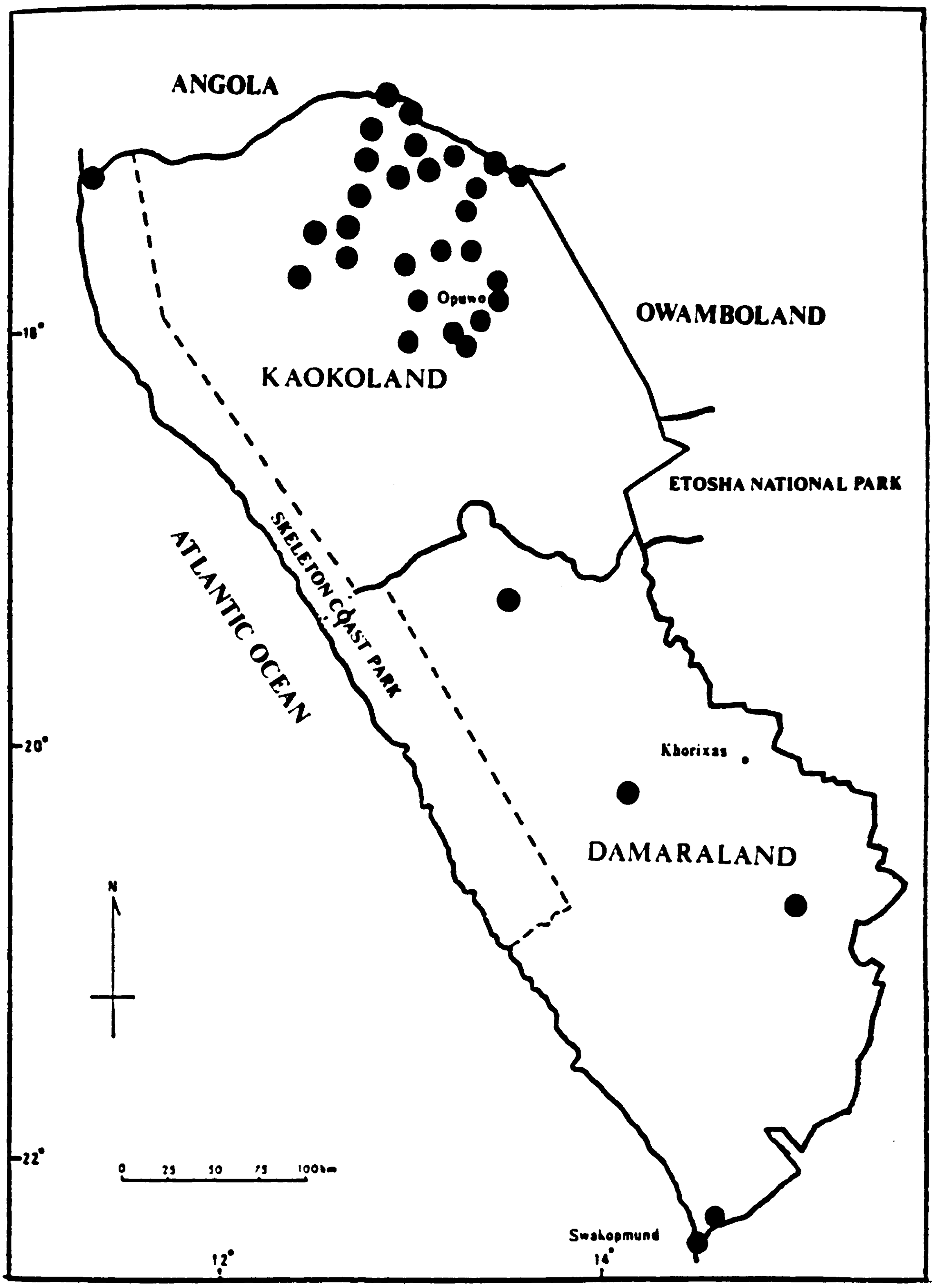


Figure 5: Definite records of elephant distribution in the Kaokoveld, South West Africa, before 1901. Compiled from the available literature (see text) together with on-site rock engravings of elephants.

divided by 28 years) and on the present yearly calving increment of 2,7 per cent for the Kaokoland (Viljoen 1980). The population growth rate is unknown and was probably negative if Shortridge's (1934) estimate of 1 000 elephants in the Kaokoveld, 34 years later is taken into acount.

DISTRIBUTION AND STATUS BETWEEN 1901 AND 1960.

Accounts of elephant distribution and numbers between 1901 and 1960 were still mostly based on short trips by various travellers to the region. There were many reliable reports, although nobody made a complete survey and large tracts of land remained unexplored. Whereas most narratives dealt with the east of the Kaokoveld, more and more travellers also moved into the west (Woods 1946, Lundholme 1951, Green 1952), reporting elephants throughout their travel routes. Again information is mostly available from incidental reports only. Where reports dealt specifically with the fauna of the Kaokoveld, many of them were based on hearsay. For example, although Shortridge (1934) stated that elephants "were widespread except along the coast", his travel routes show that he visited only the east of the Kaokoveld far from the coast.

The most comprehensive and reliable source of information on elephant distribution in the west is that of Woods (1946, 1949, 1956 and In: Green 1952) who surveyed large areas on foot. Woods reported elephants from Otjitambai, Okumutati, the Munutum River, near Angria Fria on the coast, Sanitatas, the Hoarusib River all the way to Purros, Orupembe and in the Ondondojengo Valley in the west. Other observations of elephants in the west were those of Lundholme (1951), Green (1952), and Anon (1952) during the Carp expedition in 1951. All reported elephants from Orupembe, Sanitatas and Okumutati and stated that spoor or droppings were seen over the entire region from the Kunene River to the Ugab River. March (1944) encountered elephants at the Gomatum River and at Purros.

In the east it emerged that elephants were widespread over virtually the whole Kaokoveld with the possible exception of the area south of the Ugab River. This information was compiled using the observations of Baynes (1923), Maydon (1932), Krenz (1933), Shortridge (1934), Fischer (1936), Wellington (1938), March (1944), Woods (1946, 1949, 1956 and <u>In</u>: Green 1952), Green (1952), Heck (1956), Minnaar (1957), Bigalke (1958) and De Villiers (1981), as represented in Figure 6.

There was a great difference of opinion regarding the status of these elephants and estimates range from 250 to 20 000 (Manning 1923, <u>In</u>: Shortridge 1934). In between there were the assessments by Oorlog, an Ovahimba chief in the region, who estimated 500 elephants, Steinhardt with 1 200 to 1 500 (<u>In</u> :Shortridge 1934), Shortridge (1934) with 600 to 1 000, Schoeman with 1 200 to 1 500 (<u>In</u> :Green 1952), P.Robbertse with 10 000, Woods with 600 (both <u>In</u> :Green 1952) and Bigalke (1958) with 800. From studying the

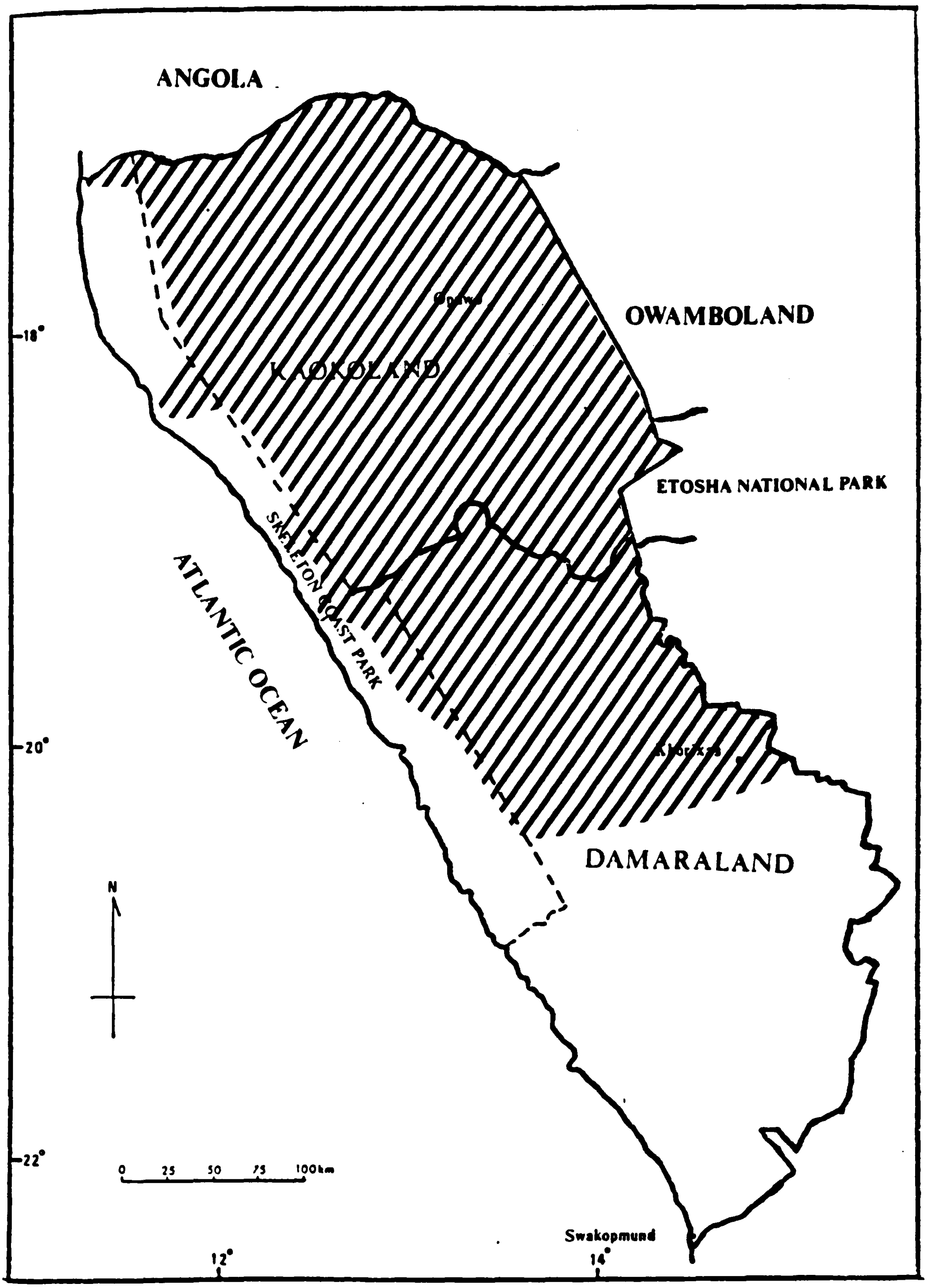


Figure 6: Known distribution of elephants in the Kaokoveld, South West Africa, between 1901 and 1960 (see text).

travel routes and time spent in the region by the various authors, it is clear that most of the above-mentioned figures must have been guesswork. Another problem was that the boundaries of what was then known as the Kaokoveld were not clearly defined and some estimates, probably that by Oorlog and Woods, only include the present-day Kaokoland, while others such as Shortridge's included the whole of Kaokoland, Damaraland and parts of the Outjo district. However, in the light of more recent surveys (Le Roux 1978, Viljoen 1980) it is concluded that there may have been anything between 600 and 1 000 elephants residing in the Kaokoveld by 1960.

Woods (In :Green 1952) was the first to distinguish between the various elephant groups and he counted 100 elephants in the Hoarusib River near Purros which he regarded as being most of the "Namib elephants". According to available records of Woods's travel routes (Woods 1946, 1949 and 1956), this probably only refers to the elephants residing in the present-day Kaokoland.

DISTRIBUTION AND STATUS BETWEEN 1961 AND 1980.

Reports for this era were the first to be based on actual counts during ground as well as aerial surveys. Some reports, however, must still have been guesswork, such as that of Odendaal (1964) who reported a total of 3 000 elephants with no sustaining surveys or references. Another problem is that most of the long-term studies were concentrated in the Kaokoland region (north of the Hoanib River) of the Kaokoveld and little information is available for the Damaraland region up to 1975.

In 1968 the first aerial survey was conducted by the then Department of Nature Conservation and Tourism, S.W.A. in which 211 elephants were counted in the Kaokoland region (Joubert 1972). In 1969, during another aerial survey, 279 elephants were counted of which 145 were seen in the west of Kaokoland, 86 in the northern drainage basin at Omuhonga and 52 in the eastern regions (Joubert 1972, De Villiers 1975). Unfortunately some confusion exists about the latter figures because different numbers are quoted in different reports concerning the same aerial survey (Joubert 1972, De Villiers 1975). As both the 1968 and 1969 surveys were less than 15 hours in duration it has to be concluded that it could only have been attempts at total counts in parts of the Kaokoland (total area is 4,9 million hectares) and that the actual numbers of elephants in Kaokoland at that time were much larger.

The latter statement is supported by a study by Owen-Smith (1970) who spent two-and-a-half years as agricultural officer in the Kaokoland region. Owen-Smith estimated the elephant population in 1970 to be between 700 and 800 of which 200 occurred in the eastern sandveld, 100 to 160 in the northern drainage basin, 200 to 300 in the subdesert region and the rest in the Beesvlakte and the mountains south of Sesfontein. Owen-Smith's (1970) detailed information on the 1970 distribution of elephants in Kaokoland is presented in Figure 7.

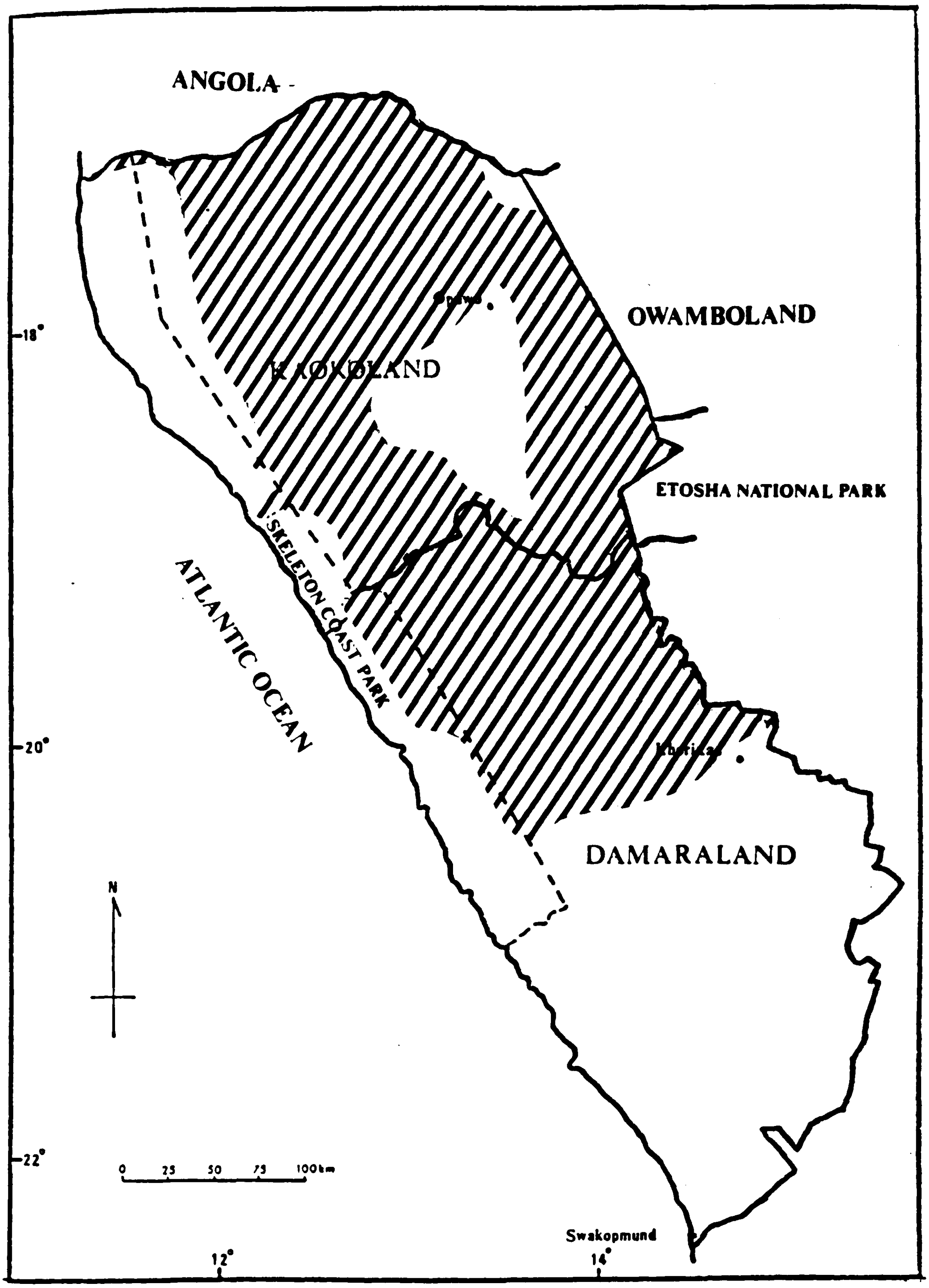


Figure 7: Distribution of elephants in the Kaokoveld, South West Africa, during 1970 (Owen-Smith 1970, Joubert and Mostert 1975).

In February 1975 another aerial survey, which included both Kaokoland and Damaraland, was conducted by the Department of Development and Co-operation. According to De Villiers (1975) 260 elephants were counted of which 190 occurred in Kaokoland and 70 in Damaraland. In the east 123 were counted with 91 in the Beesvlakte and 32 at Omumborombonga. In the western regions 137 were counted with 33 on the plains south of Sesfontein, five in the Hoanib River, 13 in the Hartmann Valley and 86 in a valley east of Sanitatas. The total duration of this survey was less than 25 hours, and large tracts, such as the eastern sandveld were not included in the survey while single transects only were flown in others. This survey can also only be regarded as a partial count yielding a minimum figure for the elephant populations.

Joubert and Mostert (1975), in their report on the distribution and status of mammals in S.W.A., stated that there were approximately 200 elephants residing in Kaokoland with another 100 to 150 in Damaraland. These numbers are probably based on the results of the previous aerial surveys (Joubert 1972, De Villiers 1975).

Between 1975 and 1977 a detailed long-term field study was undertaken to determine the distribution and status of the larger mammals in Kaokoland (Viljoen 1980, 1982a). Ground surveys were used in conjunction with three aerial surveys of 40, 25 and 25 hours duration respectively. During the first aerial survey an attempt was made to cover the whole study in wide transects, while the last two aerial surveys were intensive total count surveys of the western desert region (west of the 150 mm isohyet) of Kaokoland only (Viljoen 1982a). In total 207 different elephants were counted with a possible estimated maximum of 250 in the whole of Koakoland in 1977. This number varied seasonally because of movements of eastern elephants to and from Damaraland, Owamboland, Angola and the Etosha National Park.

During the study of Viljoen (1980) it was also found that the elephants in Kaokoland consisted of three separate geographic groups and that no contact between these groups existed. It seemed as if these three groups represented different populations, namely:

1) The northern population in the central Kunene drainage basin, which consisted of only eight cows and no bulls for at least the years 1975 to 1978. For all practical considerations (breeding potential) this group was regarded as extinct.

2) The eastern population with a minimum of 134 elephants, but with a marked seasonal fluctuation in numbers. The most westerly distribution of this population was the Kowarib Schlucht. Calves, less than one year old formed 2,7 percent of the population.

3) The western population, restricted to the area west of the 150 mm isohyet. During surveys (Viljoen 1980) a maximum of 65 elephants was counted in the Kaokoland region. No calf survived

between 1975 and 1978 and this population had a negative growth as a result of hunting.

Unfortunately the study of Viljoen (1980) only covered the Kaokoland region but one aerial survey was conducted in Damaraland in 1977 (Visagie 1977) in which 82 elephants were counted of which 59 occurred in the western desert regions. As mentioned previously a short-term survey such as the latter does not allow for conclusions and consideration of seasonal movements as borne out by the results of an aerial survey one year later in Damaraland in which 135 elephants were counted (Le Roux 1978). This latter survey is also assumed to be an undercount as the flight duration was only 10 hours.

Figure 8 is a consolidation of the 1975-1977 study in Kaokoland and the aerial surveys of Visagie (1977) and Le Roux (1978) in Damaraland. The data represent the known distribution of elephants in the Kaokoveld in 1977. A total population of 500 elephants in the Kaokoveld is suggested for this period using the information of Visagie (1977), Le Roux (1978) and Viljoen (1980). This number is supported by the findings of the present study in which 357 live elephants and 123 elephant carcasses were counted in 1983 in the Kaokoveld.

DISTRIBUTION AND STATUS BETWEEN 1981 AND 1983.

During the present study, ground surveys between 1980 and 1983 were supplemented by twelve 10-hour aerial surveys, three 25-

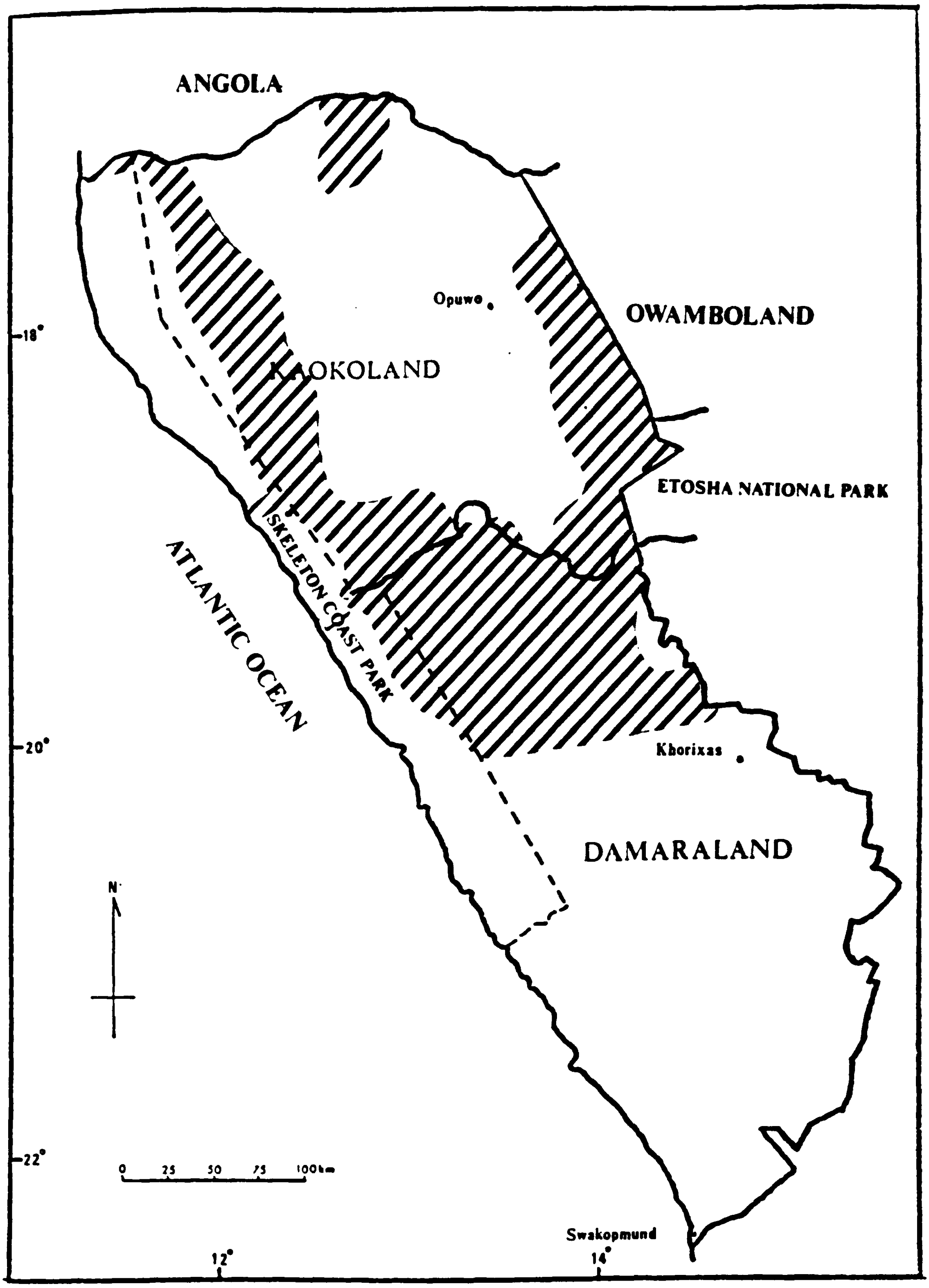


Figure 8: Distribution of elephants in the Kaokoveld, South West Africa, during 1977 (Visagie 1977, Le Roux 1978, Viljoen 1980).

hour aerial surveys and one 85-hour total aerial count (Viljoen 1982b). A total of 357 elephants was counted in the Kaokoveld in 1983. During the same period 123 elephant carcasses were found of which 107 showed positive signs of having been shot, nine having died of unknown causes, while five from the eastern population probably died as a result of the drought. In two cases the circumstances pointed to the elephants involved having been chased to death by vehicle.

As had been revealed by the study of Viljoen (1980), different elephant populations are found in Kaokoland. With the extension of the present study to include Damaraland and the Skeleton Coast Park the previous observations were confirmed: Three areas of elephant occupation in the Kaokoveld were found, one in the east, one in the west and a third concentration in the south-west (Fig. 9). In between there were areas of low or no elephant occupation. Such a situation can be brought about in two ways: Either elephants are moving seasonally between a wet and dry season range, making little use of the areas between the ranges or separate populations exist in the Kaokoveld. Since no seasonal movement between the three centres of occupance were detected during the study period it is concluded that the ranges represent three discrete elephant populations in the Kaokoveld.

These populations were identified as the eastern population, the western or desert-dwelling population and the transitional population. Each population has a definable geographical range and separate movement patterns. Also in the Kaokoveld there is a

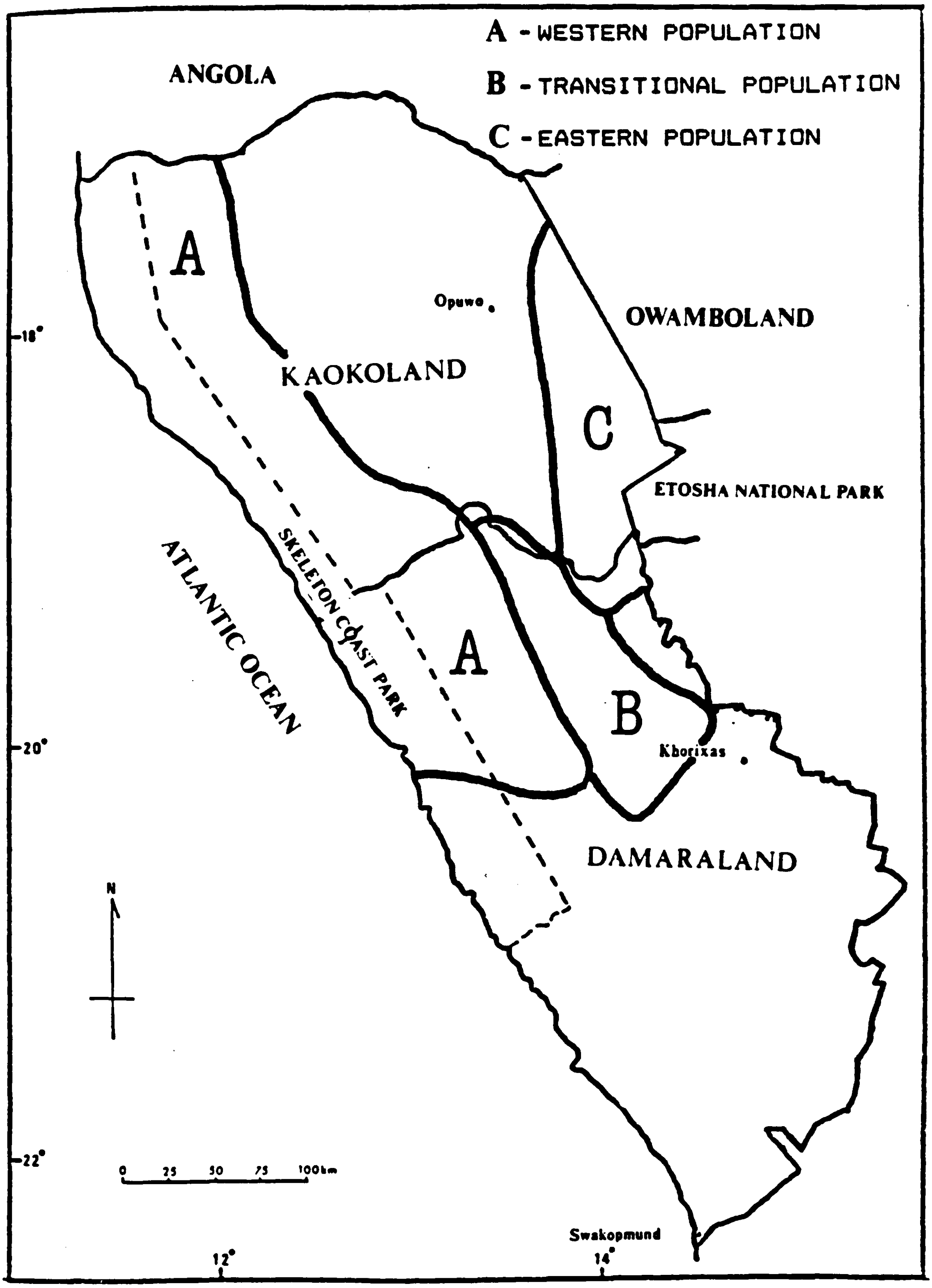


Figure 9: Ranges of the three elephant populations (heavy solid lines) within the Kaokoveld, South West Africa, during 1983.

vast difference in the range of climate and habitat occupied by the recognised populations and therefore in the survival strategies of the three elephant populations. For example the desert-dwelling elephants occupied a true desert with an annual rainfall of less than 150 mm and a vegetation density of less than one shrub per hectare whereas the eastern elephants utilized a habitat with an annual rainfall of more than 250 mm and a maximum vegetation density of 2 085 trees and shrubs per hectare (Viljoen 1980).

While no contact between the eastern and desert-dwelling elephant populations was detected during the study period, there could have been possible genetic exchange via the transitional population. This latter population made infrequent contact with the eastern and desert-dwelling populations on the fringes of their distribution range.

The remnants of the northern population in the central Kunene drainage basin (Viljoen 1980), which might once have been part of the eastern population, have since 1980 became extinct.

The distribution and status of each population will now be discussed:

1) The eastern elephant population.

This population inhabits the eastern regions of the Kaokoveld, an area bordered by Ombombo Owambo in the north, the Huab River in the south and in the west by the Joubert Mountain range extending down to the Grootberg Mountain range. A total of 207 different elephants was counted in this region with a possible maximum of 250 depending on the season. There was a marked seasonal fluctuation in the population density as these elephants migrated freely to and from the Etosha National Park and Owamboland and sometimes into the Outjo district. Movement patterns were generally orientated from north-west to south-east.

The highest concentration of 140 elephants occurred in the vicinity of Otuzemba in the eastern sandveld, with a second concentration of 50 elephants around the Ombonde River in the Beesvlakte. The calving percentage, calculated as the percentage of calves less than one year old in the whole population, was 1,9 in 1983. During the present study the elephants of the eastern population made no direct contact with the western population nor were there any western migrations or movements.

2) The western or desert-dwelling elephant population.

The focus of the distribution range of the desert-dwelling elephant population is in the northern Namib Desert region of the Kaokoveld (Chapter 2). Their distribution range is bordered in the north by the Kunene River, in the south by the Huab River, in the west by the Atlantic Ocean and in the east by a line that can be drawn roughly from the Marienfluss in the north to Die Riet on the Huab River in the south. This line also roughly corresponds with the 100 mm isohyet in its northern parts, but it extends to the 150 mm isohyet in the south.

As the present study was mainly aimed at the desert-dwelling elephant population, each of the elephants in this population was individually identified. In 1980 this population consisted of 86 individuals but in 1983 there were only 70 individuals left. This is the total known number of desert-dwelling elephants and during the study period there was no migration to areas outside this bioclimatic zone and no immigration from the east took place. The only fluctuation was at the Kunene River where the six elephants that occurred there moved freely to Angola and back. It is possible that there are more desert-dwelling elephants in the desert regions of Angola, but with the present war in the region, it was impossible to verify their existence.

Movement patterns of the desert-dwelling elephant population of the Kaokoveld were generally north-south orientated. Within the desert-dwelling elephant population five different groups were identified. they were distributed as follows :

a) Six cows utilized the Kunene River west of the Marienfluss from where they moved into the northern Hartmann Valley and southern Angola. They were more of less isolated from the rest of the population but on two occasions they moved down to the Hoarusib River to make contact with the elephants there.

b) In the Hoarusib River west of Leyland's Drift, four elephants mostly utilized this section of river but also frequently moved to the Hoanib River and up to the Khumib River.

c) The Hoanib River group consisted of 31 elephants which utilized a wide area on both sides of this river bed.

d) The Hunkab area which was mostly frequented by five adult bulls.

e) The Wêreldsend area where 24 elephants utilized the Uniab, Barab and Aub Drainages north and west of the veterinary fence.

During the 1975-1977 study (Viljoen 1980) and the present study no individual of the desert-dwelling population made direct contact with the eastern population although there was infrequent contact with the transitional population during the dry season. Between 1980 and 1983 the calving percentage was 1,38 although no calf survived as a result of illegal hunting and disturbance. In 1984 the calving percentage was 2,7 percent (S.Brain pers. comm. 1986).

3)The transitional elephant population.

The somewhat artificial classification of this population is justified by the following factors: Firstly, these elephants

S. Brain, Skeleton Coast Park, P/bag 5001, Swakopmund, S.W.A.

utilized an area on both sides of the 150 mm isohyet. They made contact with both the desert-dwelling and eastern populations on an infrequent basis. During the rainy season they moved north-east to the vicinity of Omumborombonga where they made contact with members of the eastern population. During the dry months they moved south-west where they infrequently made contact with herds of the western population. The extent of their natural movements were unclear as a veterinary line which was erected in 1976 cut right through their home ranges and disrupted their natural migration routes. With the absence of the veterinary fence it might have been possible to have made a clearer division as to the population relationship of these elephants but at present their movements are to a large extent influenced by this fence.

This population inhabits the Grootberg Mountain range area, bordered by the Omumborombonga - Khoraxa-Ams waterholes in the north, the farms Palmwag, Juriesdraai, Spaarwater and Bergsig in the west and the Huab River up to Tweelingskop and Nantis in the east. A total of 80 elephants was counted in this region during the dry season. Their calving percentage was 1,3 at the end of 1983.

The 1983 distribution of the elephants in the Kaokoveld is presented in Figure 10. As mentioned earlier this only refers to the permanent distribution of the elephants and does not include occasional infrequent movements outside permanent home ranges. For the sake of clarity the extent of these vagrant movements is

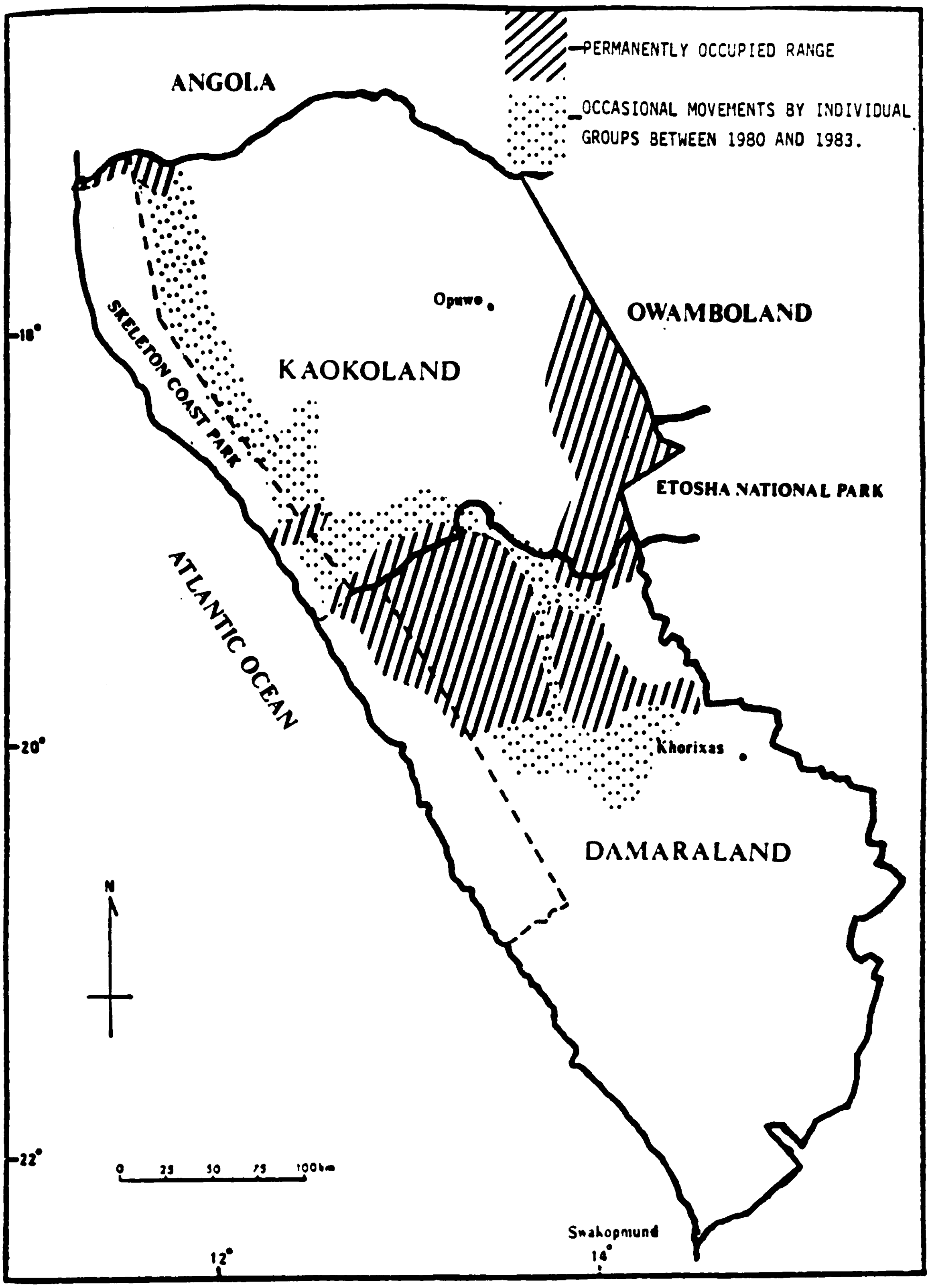


Figure 10: Distribution of the elephant (<u>Loxodonta africana</u>) in the Kaokoveld, South West Africa, during 1983.

also shown on the map. An interesting phenomenon was that even these vagrant movements never took the elephants outside the bioclimatic zones in which each population is resident.

OVERALL TREND IN NUMBERS

Despite the shortcomings of earlier descriptions and information, a clear picture emerges regarding the population trend. Prior to 1800 there is no information on the numerical status of these elephants but it is certain that they were already present in the northern Namib Desert. Round about 1880 an estimated minimum of 2500 elephants must have been in the Kaokoveld based on the number of elephants shot by the Dorslandtrekkers. Figure 11 is a graphic representation of the author's interpretation of the population trend through different time periods using the most reliable estimates. This data were compiled by using the information provided by Shortridge (1934) , Von Moltke (1945), Green (1952), Bigalke (1958), Owen-Smith (1970), Visagie (1977), Le Roux (1978), Viljoen (1980) and the present study. As can be seen from Figure 11, there probably was a sharp decline in elephant numbers after 1880, with the intensive hunting of the Dorslandtrekkers. After this period the population probably remained relatively stable until 1970 when there again was a drastic decline. This trend is even more clear when studying the various distribution maps, bearing in mind that by the time that a reduction in distribution range can be detected, there must already have been a drastic decline in population size.

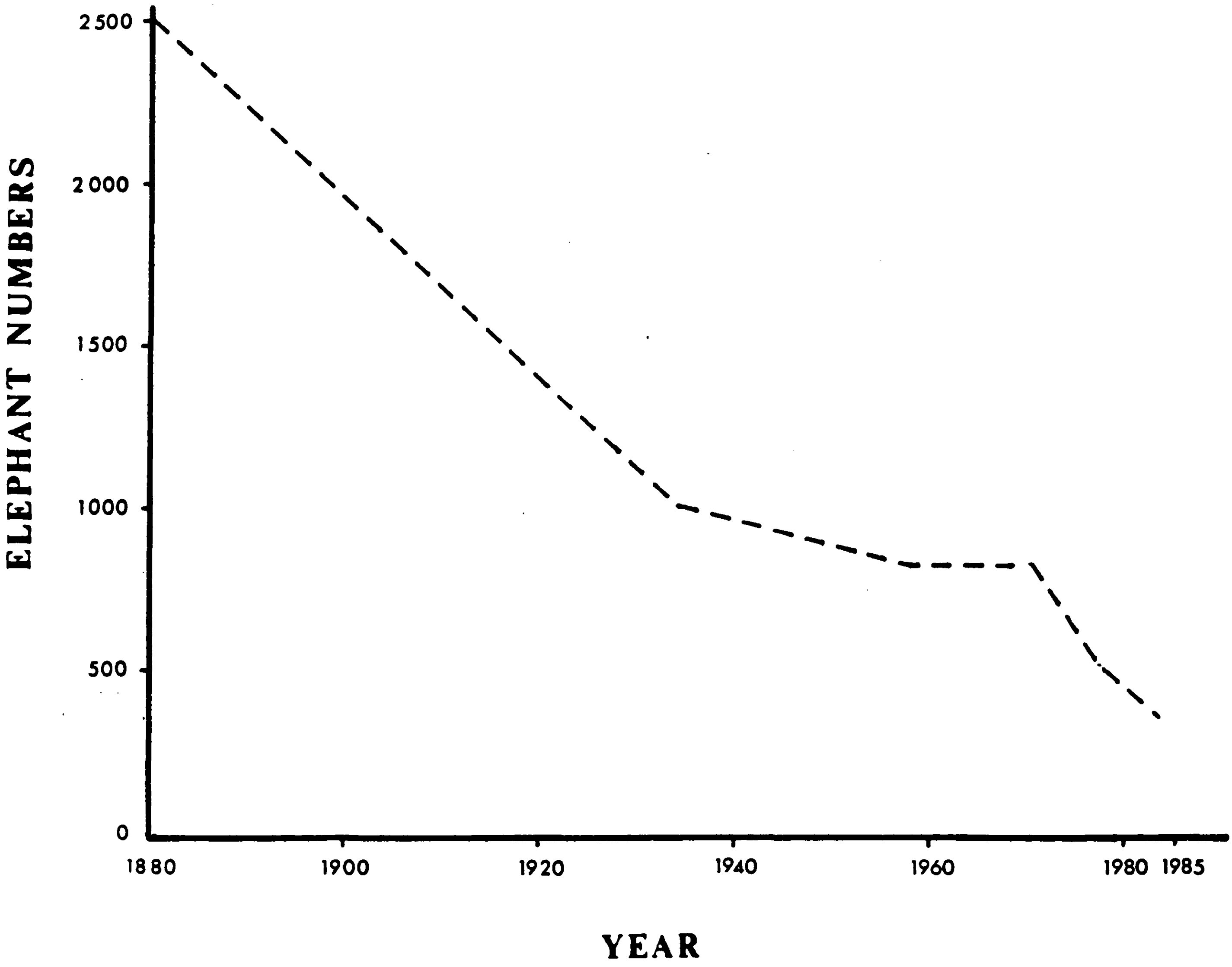


Figure 11: Postulated trend in elephant numbers in the Kaokoveld, South West Africa, since 1880, based on estimates by selected authors (see text) which are considered reliable by the current author.

The sharp decline in elephant numbers since 1970, and the shrinking distribution are especially noticeable in the Kaokoland region where the northern elephant population and the largest part of the desert-dwelling population have disappeared over a period of only seven years (Figures 7 and 8). The known northern elephant population has declined from 160 in 1970 (Owen-Smith 1970) to eight cows in 1977 (Viljoen 1980) and by 1980 they were extinct. Similarly, the desert-dwelling population had declined from 300 in 1970 to 65 in 1977 and at present there is a maximum of 39 at any one time in Kaokoland. The recent drastic decline in elephant numbers in Kaokoland is attributed to the following factors:

1) With the availability of reliable four-wheel-drive vehicles, previously inaccessible areas came within easy reach of any hunter.

2) Since about 1970 the local people (who were not regarded as hunters) were provided with guns and ammunition by the traders in Angola in exchange for ivory(B.J.Van Zyl pers. comm. 1977). This practise apparently reached large-scale proportions in the mid-1970's with the resultant extermination of the northern elephant herds.

3) More and more outsiders, who were inclined to poach and who possessed the necessary arms and ammunition, moved into the region.

B.J. van Zyl, Commissioner Kaokoland, P/bag 502, Opuwo, S.W.A.

4) Although legislation regulating hunting in the area has existed since 1907 (Wellington 1967), practically no law enforcement was applied there until fairly recently. A Nature Conservation Officer was appointed to the region in 1973 but he was stationed in Windhoek and visited the Kaokoveld only infrequently. The inaccessibility and size of the area also made law enforcement practically impossible.

5) The current war in the area has resulted in a heavy influx of weapons and people with a sharp increase in poaching and a decrease in law enforcing patrols.

6) With the abolition of permits to enter the area in 1978, there was a sharp increase in uncontrolled tourism with the resultant increase in disturbance. In an area with limited food and water resources this probably had a drastic negative effect on elephant population growth.

It was only as recent as 1982, through information supplied during the course of this study and by officials of the Namibia Wildlife Trust and the Endangered Wildlife Trust that effective law enforcement took place.

Since then the Department of Agriculture and Nature Conservation, South West Africa, has appointed more Nature Conservation officials for the region with a resultant decline in poaching. At the moment the situation is relatively stable, but with the current low numbers of these elephants this could change overnight.

HISTORICAL DISTRIBUTION OF THE DESERT-DWELLING ELEPHANTS

One of the reasons for determining the past distribution of the elephants in the Kaokoveld was to try and establish the permanency and origin of the desert-dwelling elephants. Unfortunately a satisfactory explanation regarding the origin of these elephants will probably never be found. Why and when these elephants moved into an atypical and seemingly unsuitable habitat while there was typical "elephant habitat" in the east, remains a mystery. The popular theory that these elephants were forced into the west by human activities and development in the east (Schoeman 1984), is unacceptable because of the following facts.

a) Before 1900 the human population in the Kaokoveld must have been very low (Van Warmelo 1962) and long before there was any development or large-scale hunting in the east, there were reports of elephants occurring in the west (Alexander 1838, Hartmann 1897 and 1902, Vedder 1937, Vierech and Rudner 1957). These early reports indicate that the elephants utilized all the larger river courses in South West Africa right down to the Atlantic Ocean. This might have been a seasonal occurrence, but all previous travellers in the region reported elephants in western Kaokoveld, regardless of the season. Even at present, development in the Kaokoveld is on a small scale and consists mainly of five all-weather roads, seven small schools, one veterinary fence and two hospitals.

The available information all point to a long-standing occupation of the desert by elephants, with the human factor playing a relatively small role in the distribution of these elephants, rather than the contrary.

b) The biggest recent concentration of elephants in the Kaokoveld coincides with one of the largest human settlements, at Otuzemba (Fig. 12). Here the elephants drink during the night while the waterholes are utilized during the day by the local Hereros and their domestic animals. This process has been in existence for a long time (Owen-Smith 1970) and while the elephants are hunted and harassed from time to time, they show no inclination to leave. This is in spite of the fact that the elephants involved seasonally visit the nearby Etosha National Park, but they always return to their original home ranges. There is no real factor preventing them from staying in the Etosha National Park or from moving further west.

c) The present study has shown that the elephants in the Kaokoveld show a marked attachment to their various home ranges in spite of having unlimited movement in nearly all directions. They could be driven out of their home ranges or temporarily moved out over long distances but the elephants always returned to their original home ranges. This behaviour has caused the extermination of entire herds. Examples of this are the northern elephant population which numbered 160 in 1970 (Owen-Smith 1970) only to be shot out except for eight

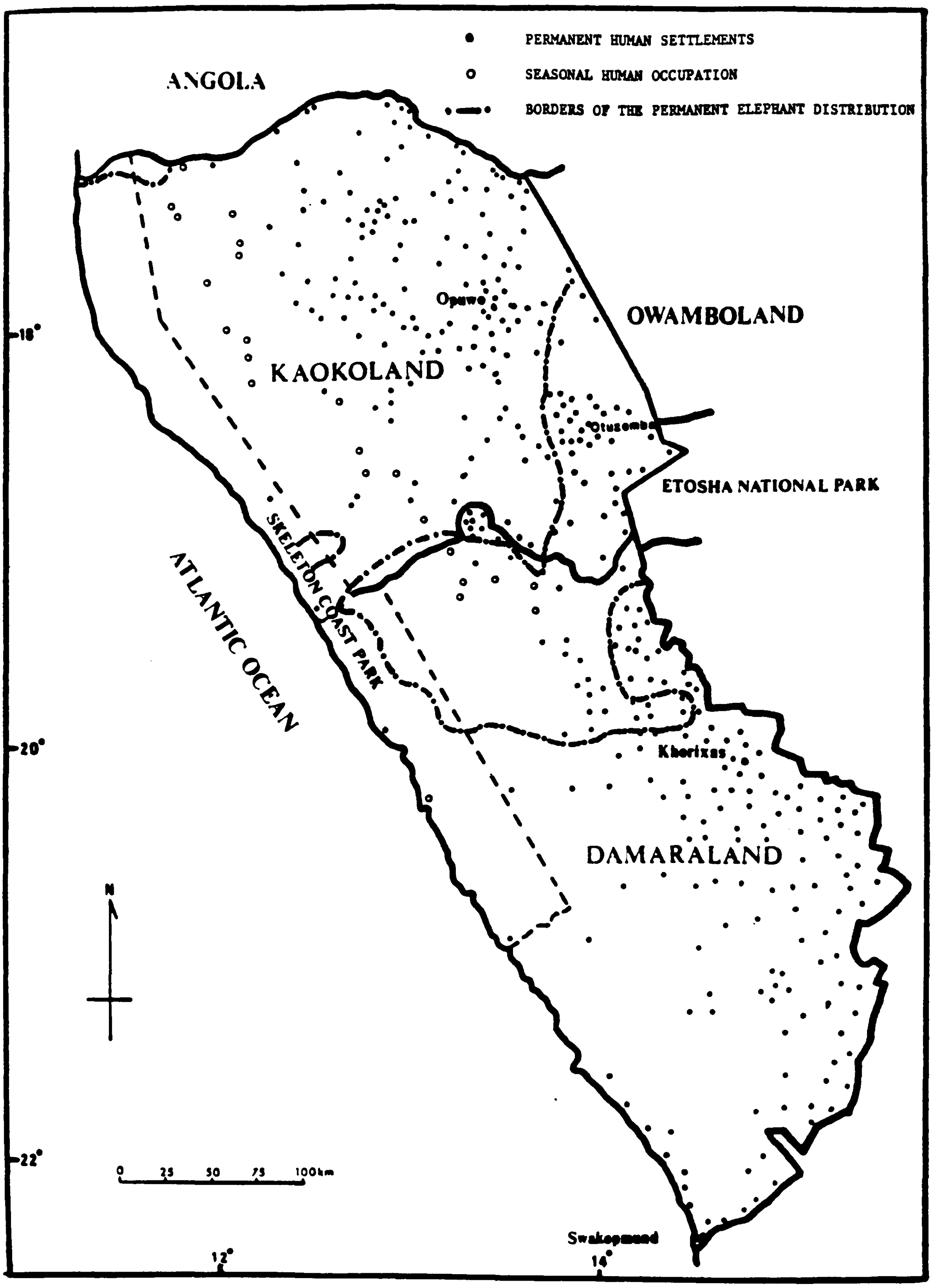


Figure 12: Current human settlements in the Kaokoveld, South West Africa, in relation to the present elephant distribution.

cows by 1977. These cows were hunted almost continuously until they too were killed in 1980 in the same area. Another example is the elephant herds of the middle Hoarusib River where Woods counted 100 elephants in 1951 (In: Green 1952) but by 1977 this group had dwindled to 14 (Viljoen 1980). In 1980 there were only four cows left who were continuously harassed and shot at by the resident people. Although these cows temporarily joined other herds for short periods they repeatedly returned to their original home range until they too were killed in April 1981. Similarly the elephants that frequented the Hartmann Valley - Kunene River region numbered 40 in 1970 (Owen-Smith 1970), eight in 1977 (Viljoen 1980) and at present consist of only six cows and no bulls. Although these cows had on two occasions joined elephants in the western Hoarusib River, they returned over a distance of 195 km to their original home range.

As there was no evidence to the contrary, i.e. no new influx of elephants and no sudden increase in numbers in a certain area, it is concluded that current gaps in the elephant distribution in the Kaokoveld were created not by forcing them out but by shooting them out.

d) In the northern Damaraland region where the highest concentration of desert-dwelling elephants still occurs, there is nothing to prevent these elephants from moving east as there is a uninhabited corridor, at the narrowest 60 km wide, from the coast right through to the Etosha National Park. In fact this corridor is used extensively by Hartmann zebras and by the elephants from the eastern population, in spite of the western fence of the Etosha National Park and one main road. The eastern elephants use this corridor to move west, up to the Kowarib Schlucht, during the rainy season and then to return east with the onset of the dry season. The desert-dwelling elephants never showed an inclination to move east out of their bioclimatic zone at any time.

It is concluded that the origin of the desert-dwelling elephants was not a recent occurrence nor was it induced by man, in fact all the available evidence points to the contrary. A possible explanation might be that it was a process of natural dispersion as a result of elephant overpopulation in the east long before the interference of man.

DISCUSSION

The main facts emerging from the data presented above concern the confirmation of the historical existence of a distinct and permanent desert-dwelling elephant population in the northern Namib Desert region of the Kaokoveld. This desert-dwelling elephant population was on the decline with a live animal: carcass ratio of 2,9:1 in 1983. The primary cause of decline seemed to be illegal hunting as 87 per cent of the dead elephants found recently have been shot.

While it is generally accepted that elephants are capable of utilizing a wide variety of habitats ranging from semi-desert with an annual rainfall of 300 mm to tropical forests with an annual rainfall of 2 000 mm or more (Laws 1970), the presence of elephants in a desert is regarded as atypical and marginal. As far as is known, such conditions exist in only two areas in Africa, namely in the northern Namib Desert of South West Africa and on the edges of the Sahara Desert in Mauritania and Mali. Little is known of the elephants in north Africa and the survival of those in Mauritania is uncertain (Douglas-Hamilton 1980). In Mali approximately 500 elephants survive in the Gourma area with an annual rainfall of between 300 and 550 mm (Guillemont 1986). These elephants reputedly move around in large herds and cover distances of 800 km (Bosman & Hall-Martin 1986). Similar to the northern Namib Desert these elephants are also dependent on food maintained by water run-off from higher rainfall areas such as the seasonal flooding of the Niger River flood plains. Another similarity is that the elephants also share the waterholes with the tribesman's cattle by drinking during the night. However, the rainfall in the northern Namib Desert is lower (<150 mm). The climatic regime of the Mali elephants, thus seems to be more on par with that of the eastern Kaokoveld (rainfall >250 mm), although the mean temperature in Mali is higher (Grove 1971) than in the Kaokoveld.

CHAPTER 4

POPULATION BIOLOGY OF THE DESERT-DWELLING ELEPHANTS

INTRODUCTION

The importance of determining the population structure and organization of free-ranging animals, and their relevance to conservation and management, requires no motivation. Characteristics of populations, and the physical condition of individuals provide basic keys as to how a population is reacting to its environment and its adaptation therein. The Kaokoveld supports one of the last free-roaming populations of elephants in southern Africa and their rapid decline in recent years warrants careful monitoring of these elephant populations to determine the vitality of these populations and to formulate reliable management policies.

The northern Namib Desert is a true desert (Louw and Seely 1982) with an annual rainfall of less than 150 mm and limited resources. This casts doubt on the elephants' permanent occupation of this area, and on their adaptation and survival in this extremely marginal habitat. The general theory has been that the elephants' utilization of this desert region is a recent and seasonal occurrence (Schoeman 1982 and 1984). However, having established beyond doubt that the elephants are permanently, and have long since been, resident in the northern Namib Desert, the aim of this investigation was to establish the population structure of elephants in the Kaokoveld, to examine their social organization, and to identify the factors which may have caused a recent decline in their numbers.

METHODS

Data on the demographic characteristics of populations may be readily obtained where destructive sampling of a population is possible. Where data of this sort cannot be collected, the necessary information can only be obtained by detailed long-term observations of the species. The elephants of the Kaokoveld fall into this latter category. Where necessary, the motivation for a particular method employed is discussed under the appropiate heading.

POPULATION SURVEYS

Between April 1981 and January 1983, 17 aerial surveys were conducted in the Kaokoveld. These surveys varied from 10 to 85 hours in duration. Four aerial surveys covered the distribution range of all three elephant populations in the Kaokoveld while the remaining surveys were restricted to the range of the desert-dwelling elephant population. From August 1981 to January 1983 aerial surveys were conducted at monthly intervals.

Systematic sample aerial surveys gave erroneous results due to the heterogeneous topography of the study area and the clumped distribution of the elephant population. Instead, during each survey an attempt was made to locate all known individuals within the desert-dwelling population rather than to do systematic sample counts. The area to be surveyed was examined along a series of predetermined flight paths, first covering the major river courses and water-holes within the elephants' distribution range and then actively searching for individually known elephants not found along the regular flight lines. The latter often involved following spoor from the aircraft, usually starting in the area where the elephants were previously known to have been. Outside river courses and sandy areas, tracks remained visible for up to six months in the arid climate, and because of the low vegetation density, were clearly visible from the air. In fact it was often easier to follow spoor from the air than from the ground.

The aircraft used was either a high-wing Cessna 182 or a low-wing Piper Commanche and apart from the pilot, there was a minimum of two observers, one of whom always was intimately familiar with the terrain. Observations were made from a height of 80 to 200 m above ground at an indicated air speed of between 80 and 120 km/h. Flying was restricted to the early morning from 07h00 to 10h00 and the late afternoon from 16h00 to 18h30 so as to utilize optimum visibility conditions. The numbers, location, habitat and group size of all elephants were recorded on a handheld tape recorder and plotted on a 1:250 000 topographical map. Because of the small elephant population it was often possible to identify individuals or family groups with conspicuous markings from the air. To facilitate identification at such times, flying speed was reduced to 80 km/h at a height of 80 m above ground.

Aerial surveys were supplemented by systematic ground surveys. Also, extended field surveys were conducted in the periods between the regular monthly aerial surveys. This involved following individual elephants or groups for up to 14 days at a time, noting all relevant information. To minimize bias in the analysis of seasonal distribution, habitat utilization, group sizes, movements and space use patterns, only the first observation of an individual elephant or group in any one month was used in the analysis.

INDIVIDUAL IDENTIFICATION

Individual elephants were recognised by natural characteristics such as broken or unusually-shaped tusks, cuts or holes in the ears, patterns of tail hair, etc. (Douglas-Hamilton 1972, Croze 1974a, Leuthold 1977). The variation in the type of distinctive marks or a combination thereof, resulted in a virtually infinite combination of markings and consequently the chance of confusing two elephants was negligible. A photograph of each individual elephant was filed in a reference book, suitable for carrying in the field. This book also contained information on age, sex, associations with other elephants, etc.

In 1980 a total of 86 individual desert-dwelling elephants were identified in this way. During intensive ground patrols and scanning during flights, these known individuals were frequently encountered and it was assumed that the same would have been true for unidentified or strange elephants in the same area. Consequently, the possibility of unidentified or immigrant elephants being unnoticed in the census area was believed to be minimal. The above-mentioned 86 elephants were thus considered to represent the total desert-dwelling elephant population in 1980. In 1982 the population was reduced to 70 and most of the parameters discussed in this study consequently represent the latter 70 elephants.

SEX DETERMINATION

Sex determination of living elephants

The external genitalia of an elephant sit low and between the hind legs. They are not easy to see and if visible often cannot be differentiated because the penis is usually retracted while matters are further complicated by the relatively large clitoris of the female (Kerr 1978). Alternative field methods have been developed to differentiate between the sexes, one of which being that the sex of a living elephant is determined by the outline of the forehead. The forehead of the female has a distinct angle as opposed to that of bulls in which the forehead curves smoothly downward (Sikes 1967, Barnes 1979, Hanks 1979, Smithers 1983). In another method the circumference of the tusk in relation to its length is used to distinguish between the sexes of elephants

(Laws 1966 and 1969a, Corfield 1973, Pilgram and Western 1986). In practise it proved to be easy to distinguish sexes in adult elephants on account of the above field methods and also based on the growth form and size.

However, while the above methods hold true for adult elephants, it all breaks down where younger elephants are concerned. In the Kaokoveld it was found that reliable sexing of young elephants is only possible by observing each elephant when it was urinating at a time when the elephant is undisturbed. The presence of the extended penis or lack of it then indicates the sex of the individual concerned. In this way all the known living elephants of the desert-dwelling elephant population were sexed. While an attempt was made to establish the sexes of younger elephants in the eastern and transitional elephant populations during monthly aerial and ground surveys, it proved to be unreliable in want of prolonged observations of each individual elephant in the latter populations.

Sex determination of elephant carcasses

Determining the sex of a decomposed elephant carcass also presented a problem. Accurate height measurements were impossible and as most carcasses were of elephants that had been shot, the tusks were sawn or chopped out. This destroyed the tusk cavities, the size of which could have indicated the sex of the relevant carcass (Corfield 1973). As an alternative sex determination method the possible relationship between age-specific mandible size and sex from elephants of known sex and age was investigated. Various measurements were tested but most measurements could not be made consistently, such as mandible height, or could only be applied to a limited number of mandibles as parts of the mandibles were damaged. Especially, the symphysis mandibulae and the mandibular condyle as well as the posterior bulge of the mandible were often damaged in transit or by predators. Thus the measurement of the length of a mandible as applied by Laws, Parker and Johnstone (1975), who used fresh mandibles from culled carcasses, could not be made of the majority of mandibles found in the Kaokoveld. The only reliable consistent measurement which could be applied to all mandibles of which the two halves were still attached, was the width of the mandible. This measurement was taken on the insides of the two halves, directly beneath the mandibular condyle. The measurements of mandibles from elephants of known sex and age were then tested for a possible relationship between mandible width at age and sex.

SOCIAL ORGANIZATION

Group size

Elephant group sizes were determined to examine the social system of the elephants and also to identify possible environmental influences on their social organization.

The term 'group', as used in this study, is defined operationally as any number of elephants that are closely associated in space and appear to be fairly coordinated in their activity at the time of observation (Leuthold 1976a). It does not imply specific social ties. In particular, it is not synonymous with the 'family unit' characteristic of elephant social organization (Laws 1969a, Douglas-Hamilton 1972). Single animals are treated as a 'group' throughout. Group size data were collected for each month and were analysed on the basis of the wet, cold dry and hot dry seasons for each year separately to compare the overall changes on a seasonal and yearly basis.

Group organization

The frequency and composition of elephant groups were constructed from observations made between June 1980 and January 1983. Groups were separated into units containing only adult bulls and units containing females of all ages and young males. In this context the basic unit of elephant social organization was studied. First defined by Buss (1961) and later confirmed by other independent studies (Laws 1970, Douglas-Hamilton 1972, Martin 1978, Santiapillai, Chambers and Ishwaran 1984), the basic unit in an elephant population is described as a family group or a unit which numbers from three to 15 individuals and consists of females, apparently related to each other, and their offspring, forming a closely associated group at all times, although they may temporarily join other family groups.

Operationally, the basic family unit in this study is defined as the maximum number of individuals which forms a close association especially during times of stress (e.g. dry season) and which are always coordinated in their movements and geographical range.

Each elephant was individually identified as previously described. The structure and composition of each family unit were then determined by long-term field observations. Individual elephants of each group were first classified into field age classes as described by Laws (1966) and later refined to height-age classes by the photographic measuring method as described later on.

Associations between groups and individual animals were tested for significance by a 2 * 2 contingency table using the chi-square technique (Cole 1949). Only animals for which adequate sample sizes were obtained, were used in the calculations of association.

AGE DETERMINATION

The age structure of the desert-dwelling elephant population was analysed through the following steps;

1) Measuring the shoulder-height of the living elephants.
2) Relating the shoulder-height of the living elephants to age.
3) Determining the molar ages of lower jaws found in the field.

4) Combining the estimated ages of the living elephants and the molar ages of found lower jaws from elephants that were shot to obtain a representative sample of the natural age structure of the desert-dwelling elephant population.

5) Using field age criteria for comparison with other populations.

Age determination of the living elephants

If a living elephant could be measured reliably and the dimension obtained be related to age, it should be possible to work out age structures of living elephant populations. Laws (1969a), Krumrey and Buss (1968), Hanks (1972a), Laws _et al_. (1975), Lang (1980) have investigated the relationships between the shoulder height and the age of elephants. It appears to be a reliable parameter for describing linear growth of elephants as there is relatively little variation at age. Thus if the shoulder height is known, the age of an elephant can be estimated.

In order to measure the shoulder height of a living elephant, the pole method as advocated by Douglas-Hamilton (1972) and Jachmann (1980) was used. In this method the lateral view of an elephant is photographed and when the elephant has moved away, a second photograph is taken of a measuring pole, marked in 50 mm intervals, at the same spot. Care was exercised in placing the measuring pole at exactly the same spot as the elephant's front foot. This spot was indicated by the front spoor of the elephant. Also, the position and angle of the camera during the first photograph is duplicated exactly.

Paired negatives are then projected on to a wall to give images on the same scale up to 500 mm high. The shoulder height of the elephant, measured from the edge of sole of the front foot to the crest of the scapula (Johnson and Buss 1965, Laws 1966, Elder and Rodgers 1974), is then marked on paper and compared to the dimensions of the measuring pole on the second negative as measured to the nearest 1,0 mm. The true height of the elephant is then calculated according to the projected scale of the measuring pole.

In this study the pole method proved to be superior to other methods which implement range finders, sliding rules or calculations based on the focal length of the camera, in terms of accuracy, cost and ease of operation. Due to the expense and fragility of equipment required to do stereo photogrammetric measurements (Douglas-Hamilton 1972, Hall-Martin and Ruther 1979), this latter method was not tested in this study. The pole method does not require a prolonged period in which the elephant must stand in one place in order to be measured - the elephant can be "captured" in an instant and the second photograph taken at ease, a facility which is important when working with wary elephants. The accuracy of the method depend on the posture of the animal (e.g. standing, walking or running), of placing the measuring pole at the exact spot where the elephant had stood, and by the care exercised in not letting the pole end sink into the sand. Comparison with known height objects (n=7) indicate a total error in height of less than two per cent. However, according to Jachmann (1980) the total error in height obtained by the pole method is approximately 6 per cent.

The measured shoulder-heights of the elephants were then compared to those of known-age elephants to relate them to predicted ages.

Age determination of elephant carcasses

The currently accepted criterion for ageing African elephants is the degree of molar replacement. It is generally agreed that the molar progression is essentially an intrinsic physiological process of growth independent of the process of wear and thus relatively constant in different populations (Johnson and Buss 1965, Laws 1966, Sikes 1966 and 1968, Krumrey and Buss 1968, Hanks 1972a, Fatti, Smuts, Starfield and Spurdle 1980). Two methods have been widely accepted and are generally used (Lark 1984, Jachmann 1985). They are:

a) The foramen mentale (FM) technique and age estimation reference chart of Sikes (1966 and 1968) where age is determined by the number of lamellae that, during the process of growth, passes the foramen mentale, a hole in the lower jaw.

b) The pictorial age scale of Laws (1966) which uses thirty more or less arbitrarily assigned age classes, each with a specific diagramme of tooth eruption and wear.

Both methods have certain intrinsic difficulties, but because there are no reliable alternative methods, these two methods were both tested in the current study as to ease of operation and reliability. Although Laws' (1966) technique is known to give artificial peaks and troughs in age distribution curves for populations (Hanks 1972a, Fatti *et al.* 1980, Jachmann 1985), Laws' technique is nevertheless adapted for use in the present study for the following reasons:

Laws' technique proved to be easily applied in the field and the pictorial identification of molars left no doubt as to the assigned molar, making classification of molars and therefore age classes, if not absolute ages, exact.

In contrast, Sikes' (1966 and 1968) technique assumes that each of the six molars has a constant number of lamellae throughout the population, but this is by no means certain (Laws 1966, Hanks 1972c, Lark 1984). Thus, the true foramen mentale formula could vary from that calculated by counting forward from the posterior lamella. Also, although Sikes (1971) stated that a divided foramen mentale is only occasionally encountered, this is not the case in the Kaokoveld as 40,0 per cent of the right mandibles and 20,5 per cent of the left mandibles had more than one hole in the position of the foramen mentale. A further 2,2 per cent of the mandibles had three holes. In 37,2 per cent of the mandibles examined, there were different numbers of holes representing the foramen mentale in the right and left mandible. Thus the exact position of the foramen mentale could not always be determined with absolute certainty and different ages were obtained for the same elephant, using either the right or left mandible. Therefore, molar age classification according to Sikes' technique proved to be doubtful in a relatively large percentage of cases and was abandoned in favour of Laws' technique.

Mandibles were collected throughout the study area and marked with a waterproof paint. Apart from fresh elephant carcasses encountered, the approximate time of death of older carcasses was determined by comparison to carcasses from elephants of which the time of death is known. The presence of dried flesh, or in the absence of flesh, the degree of weathering of the bone such as cracks and crumbling were used as a subjective criterion to determine the approximate time of death of the elephant involved. Those judged to represent pre-1979 deaths were excluded from the calculations since the year of death of old weathered bones could not be determined. Molars in each mandible were identified and the degree of molar replacement recorded, using the technique of Laws (1966) for subsequent ageing. The ages of mandibles believed to be from elephants that had died during 1979, 1980 and 1981 were adjusted by a factor of plus three years, two years and one year to make them compatible with the data collected in the base year of 1982.

Field age determination

For comparative purposes, the population size and structure of all three identified elephant populations in the Kaokoveld were determined by monthly aerial and ground surveys as described previously. Ageing was based on subjective shoulder-height approximates based on Laws' (1966) field age criteria. To minimize subjectivity the age-height classes were simplified as follows:

Calves: up to 1 year of age: i.e: calves up to 1,14 m in shoulder height which are able to walk under their mothers.

Juveniles: up to 3 years old with a shoulder height up to 1,5 m and which reaches up to their mother's mouth.

Immatures: up to 10 years old with a shoulder height up to 1,85 m which reaches up to the mother's eyes.

Subadults: up to 15 years old and a shoulder height up to 2,18 m.

Adults: all elephants older than 15 years with a shoulder height higher than 2,18 m.

By comparing photographic measurements of the shoulder heights in the desert-dwelling elephant population with the field age estimates of the same elephants during ground and aerial surveys, it was clear that adults and subadults, because of the relatively small height differences in the older age classes, could not be reliably and objectively distinguished from each other during field age estimates. Especially in small elephant groups, where all height classes are not present, the field age method can be very subjective. Therefore, to limit bias, no distinction was made between the latter two age classes in the comparative analysis of the different elephant populations in the Kaokoveld.

Also, as described earlier, without a prolonged period of observation, sex determination in the younger age classes was unreliable. Thus, during the relatively superficial ground and aerial surveys, sexes could only be reliably differentiated between older cows and mature bulls older than 22 years of age. The latter age corresponds with a shoulder height of 2,6 m, the height at with bulls surpass the shoulder height of cows. In the comparison of elephant populations, therefore, no distinction is made between males and females of the younger age classes.

AGE AT SEXUAL MATURITY AND CALVING INTERVAL

Birth rate and age at sexual maturity are rated to be some of the most important indicators of the demographic status of an elephant population (Buss and Savidge 1966, Laws 1966, Douglas-Hamilton 1972, Hanks 1973). The above parameters in other elephant populations have mostly been obtained through destructive sampling by autopsies (Buss and Smith 1966, Laws 1966, 1969b, Hanks 1972b, Smuts 1975). Since destructive sampling could not be applied in the present study, indirect methods had to be employed in order to give an indication of age at sexual maturity and calving interval.

The methods employed by Douglas-Hamilton (1972) and Jachmann (1980) in which the mean calving interval is determined by calculating the mean age interval of the calves that accompanied a cow and the method of sexual maturity calculated by subtracting the age and gestation period of the oldest calf from the age of the mother, are judged to be inapplicable in the present study for the following reasons: The 1982 age structures of most family units identified in the desert-dwelling elephant population suggest that one or more of the older females is missing from the respective family units. This is supported by the large proportion of females (31 per cent) older than 30 years, possible matriarchs, which were killed between 1979 and 1981. Since poachers would tend to select animals with large tusks, e.g. bulls and older cows, and since matriarchs tend to expose themselves by their altruistic behaviour (Dublin 1983), it is reasonable to assume that many matriarchs could have been killed by poachers. Furthermore, while the relationship between suckling calves up to approximately three years of age and their mothers could be established with reasonable certainty, it was difficult to establish the relationships of older calves and hence the calving intervals of individual cows. This is because in older calves it was difficult to detect a strong relationship between any one cow in a family unit and also because factors such as allomothering (Sikes 1971, Douglas-Hamilton 1972, Dublin 1983), adoption and neonatal mortality as well as bull calves leaving the family unit, would tend to make deductions about older cow-offspring relationships doubtful.

In this study therefore, possible age at sexual maturity was determined by recording only young females with presumably their first calf (where there is no doubt as to the mother-calf relationship) and subtracting the gestation period of 22 months and the age of the calf from that of its mother to arrive at the age of first conception of the individual cow.

In establishing calving interval, the only feasible method was to record the number of surviving calves present in the population during a specific year as a factor of the number of mature females present in the population during that year. Thus, for any particular year the number of mature females in the population divided by the number of calves-of-the-year gives an estimate of the calving interval (Croze 1972). The mean calving interval was estimated by dividing the cumulative yearly totals of mature females in the population over a period of time by the total number of calves surviving in that same period of time, where:

F_x = Number of mature females in the population during a specific year.

C_x = Number of calves-of-the-year in the population during a specific year.

$$\text{Mean calving interval} = \frac{F_1 + F_2 + F_3 + \ldots\ldots F_x}{C_1 + C_2 + C_3 + \ldots\ldots C_x}$$

Due to the nature of this study and the small size of the population concerned, more reliable data are not available and both the age at sexual maturity and mean calving interval should be considered as rough estimates especially since possible calf mortality is unknown.

ANALYSIS OF DATA

Different parameters were used to analyse and interpret the data. Analyses were conducted according to the methods used by Simpson, Roe and Lewontin (1960), Mulholland and Jones (1971), Welkowitz, Ewen and Cohen (1971) and Caughley (1977). To test the different hypotheses, the following statistical tests were used:

1) Chi-square (X^2) - to decide whether an observed series of frequencies of occurrence differed significantly from those expected.

2) T-test - to test for significant differences between the means of two sets of observations.

3) F-test (ANOVA) - to test for significance between three or more sets of observations.

4) Linear correlation coefficient (r) - to test the linear relationship between two variables.

All tests were two-tailed and the probability of significance was set at the five per cent level ($\alpha = 0{,}05$). To study and interpret differences and tendencies in variables, parameters such as mean ($\bar{X}$), standard deviation (SD), range, coefficient of variation (CV) and percentage frequencies were used.

A single parameter might be misleading. For example, the mean of a sample might be nothing else than a mathematical number where there is a great variance. Combined with other parameters such as standard deviation which is an indication of variance in a sample, range which shows the maximum and minimum values and coefficient of variance which indicate the relative variance in a sample, it facilitates in interpreting tendencies. Where samples differ in time and space, data were converted to percentages to facilitate comparisons. Other means of analysing data which were related to a specific sample will be discussed under the appropriate headings.

RESULTS

SOCIAL ORGANIZATION

Group size

The mean group size of the desert-dwelling elephant population of the northern Namib Desert during 1981 - 1982 was 5,03 ± 4,97 (n = 1144). However, cursory inspection of the original count data, as well as extended field observations, revealed that the group sizes of the elephants fluctuated considerably as was also indicated by a coefficient of variation of 226,0 per cent.

Table 4 presents data on group sizes for each season during 1981 and 1982 respectively. Inspection of Table 4 reveals a definite pattern with the highest mean group sizes recorded in the wet seasons and a gradual decrease during the cold dry seasons to reach a minimum group size with the smallest variation in the hot dry seasons. Group sizes during 1981 ($\bar{X}$ = 4,44 ± 3,87; n = 113) were generally smaller than those of 1982 ($\bar{X}$ = 5,61 ± 5,81; n =

Table 4: Comparison between group sizes of the desert-dwelling elephants of the northern Namib Desert, South West Africa, during different time periods.

SEASONS	MEAN GROUP SIZE	n	SD	CV	RANGE	t-TEST VALUE	DF	P VALUE
Wet 1981	6,69	13	7,85	117	1-25	-0,71	22	>0,05
Wet 1982	9,36	11	9,83	105	1-25			
Cold Dry 1981	4,40	20	3,33	76	1-14	-1,08	52	>0,05
Cold Dry 1982	6,20	34	6,91	111	1-27			
Hot Dry 1981	4,09	80	2,89	70	1-11	-1,13	147	>0,05
Hot Dry 1982	4,72	69	3,95	84	1-17			

SD= Standard deviation. CV= Percentage coefficient of variation.

DF= Degrees of freedom

114), although there were no significant differences in group sizes between the two years (t = 1,776; p>0,05; df = 225).

From Table 4 it can also be seen that there were no significant differences in group sizes between corresponding seasons in successive years. Thus, for comparative purposes the data of 1981 and 1982 are pooled in Figure 13 which represents the seasonal frequency of elephant group sizes and the percentage of the desert-dwelling elephant population associated with a specific group size. For the different seasons the group sizes differed significantly between the wet and hot dry seasons (t = 3,519; p<0,001; df = 171) but there were no significant differences between the cold dry and hot dry seasons (t = 1,775; p>0,05; df = 201) and likewise between the wet and cold dry seasons (t = 1,374; p>0,05; df = 76).

Inspection of Figure 13 reveals that during the wet season, groups larger than 21 occurred in the highest frequency and that most of the elephants in the desert-dwelling population were associated with these large herds. During the cold dry season there was a marked reduction in the incidence of large groups although a high proportion of the population still occurred in large herds. In the hot dry season, however, large groups broke up with a corresponding increase in smaller groups. During the latter season the population was also more or less evenly distributed among the various group sizes.

This seasonality in group size implies a positive relationship

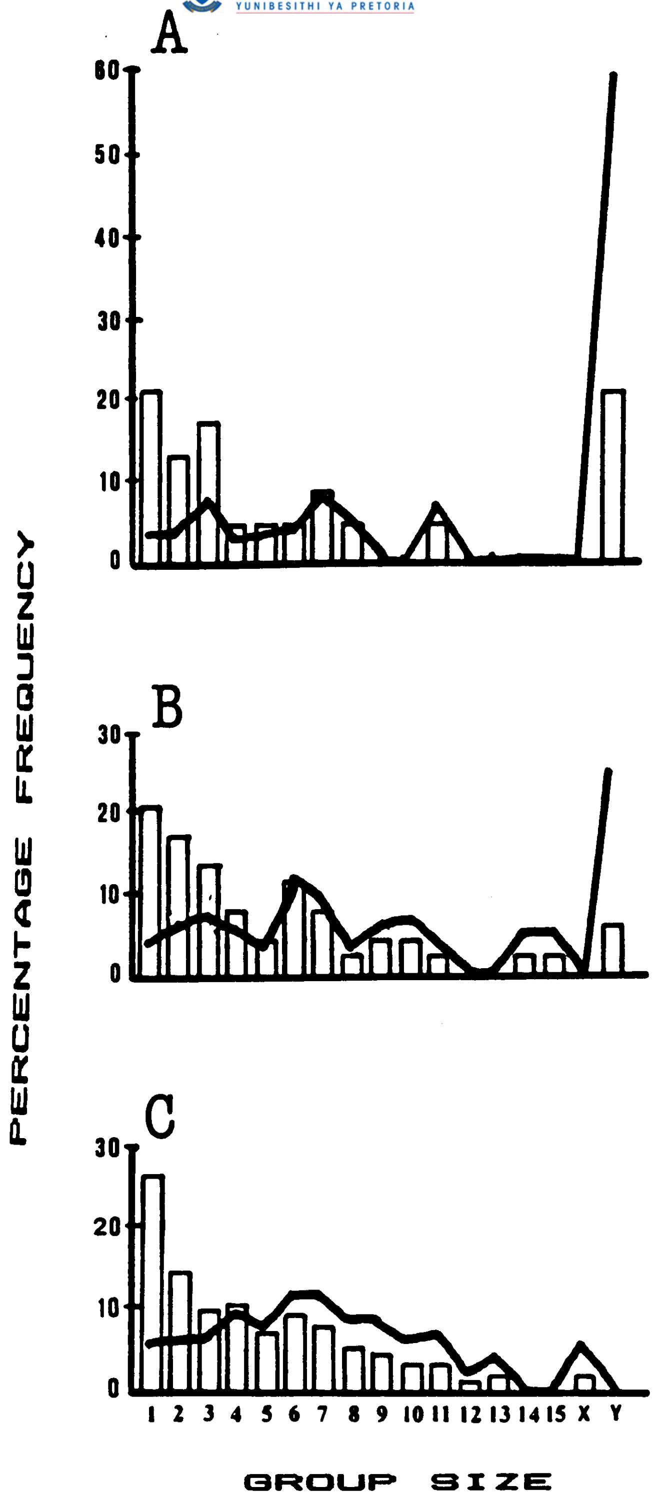


Figure 13: Seasonal frequency distribution of group sizes and the percentage (heavy black lines) of the desert-dwelling elephant population associated with a given group size in (A) the wet season, (B) the cold dry season and (C) the hot dry season in the northern Namib Desert, South West Africa. X = group size of 16-20 and Y = group size of 21+.

with rainfall. However, there was no significant linear correlation between monthly rainfall and monthly mean group size (r = 0,28; t = 1,386; p>0,05; df = 23). Matters were further complicated by the fact that no rain fell during 1981, while in 1982 the total rainfall was 94,0 per cent above the long-term average for the region. This suggested that group sizes were regulated by some factors other than climate. However, field observations showed that large herds were almost always associated with areas with green vegetation. Even in 1981, when no rain fell in the northern Namib Desert, the flooding of the major river courses because of rainfall in the eastern catchment basins, resulted in a flush of green vegetation in the western courses of the rivers. It seems therefore, that it is not the rainfall itself, but the effect of the rainfall and river-floods on the vegetation which might influence elephant group size. Thus, by allocating an arbitrary rainfall value to river-floods, equal to the minimum amount of rainfall in the eastern catchment basins to induce river-floods in the west (68 mm), and by comparing the previous month's rainfall with mean monthly group size (Fig. 14), a significant linear correlation was found (r = 0,53; t = 2,968; p<0,01; df = 23).

This indicated that there is a positive linear correlation between the effect of rainfall on the vegetation over a period of time and subsequent elephant group sizes. Although there were exceptions, mainly due to the temporary nature of large groups, it appears then that seasonal variation in elephant group size is not governed by some inherent social function. This is illustrated in Figure 14 where the formation of large groups generally trail the

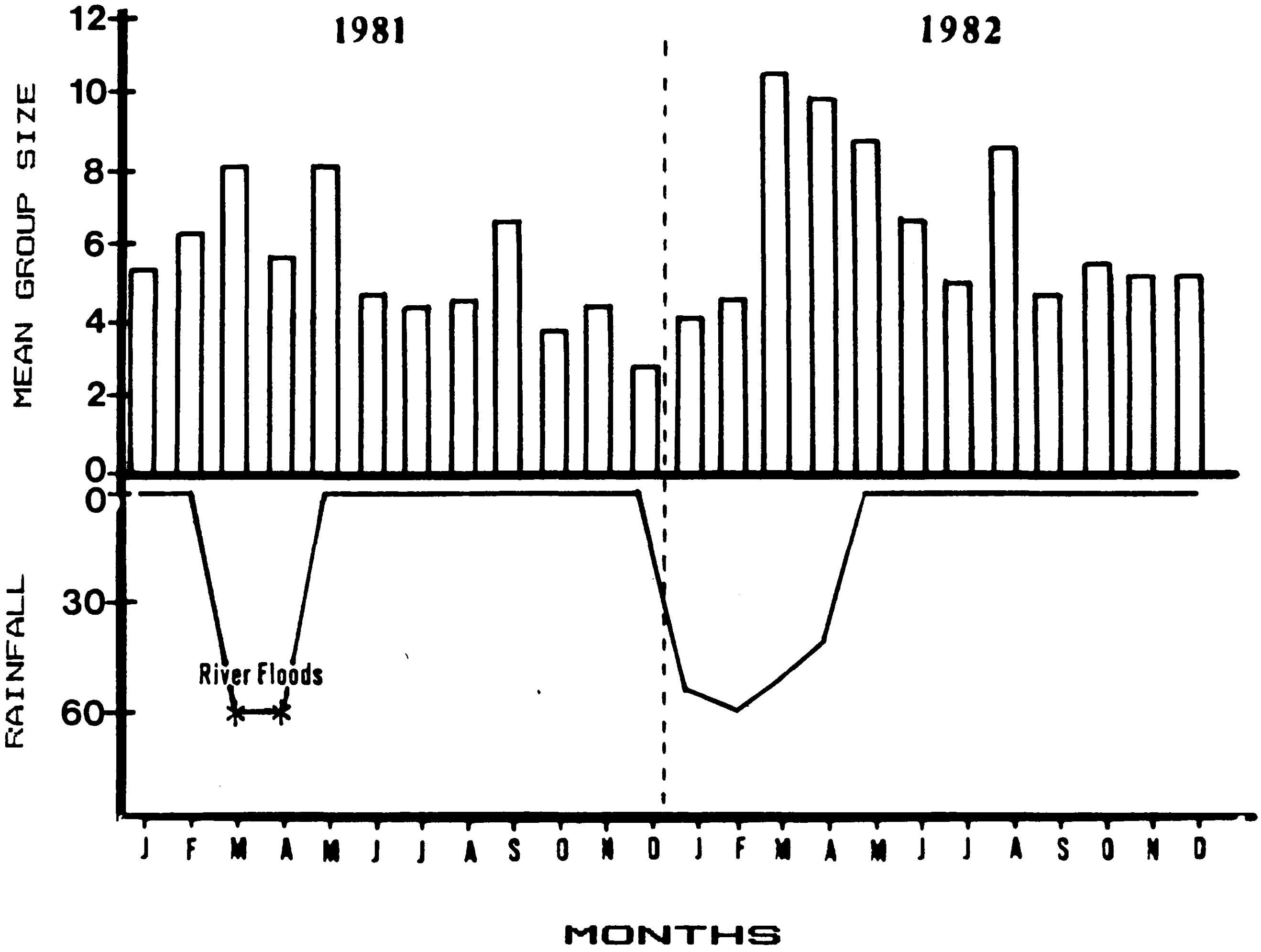


Figure 14: Comparison of mean monthly group sizes in the desert-dwelling elephant population with rainfall (mm) and the occurrence of river floods in the northern Namib Desert, South West Africa, during 1981 and 1982.

rainfall by one month. The dependence of large groups on green vegetation is further highlighted by the differences in mean monthly group sizes between 1981 and 1982. In 1981, when river-floods produced a limited supply of green vegetation which deteriorated rapidly, mean group sizes were lower than in 1982 and large groups broke up rapidly so that mean group sizes in the cold dry season were little different from that of the hot dry season in 1981. In 1982, by contrast, widespread rains resulted in an abundance of green vegetation which lasted well into the cold dry season as reflected by the large elephant groups in the 1982 cold dry season.

The wet season congregation of elephants is regarded as 'feeding assemblies or aggregations' (Douglas-Hamilton 1972, Barnes 1979) of several elephant family units in areas of choice food plants. This is confirmed by a positive linear correlation between the previous month's rainfall and the percentage of elephants found in groups larger than 10 ($r = 0,79$; $t = 4,821$; $p<0,001$; $df = 23$). As the largest family unit identified in the desert-dwelling elephant population consisted of 10 animals, this confirms that the cause of increased mean group size is indeed aggregations of several family units into relatively large feeding groups after rainfall (i.e. at areas of green vegetation), as was also evident from more casual observations.

Family units

The desert-dwelling elephant population of the northern Namib Desert basically consists of three elephant units, i.e: all male groups or bull groups, mixed groups and single animals. Mixed groups consist of females of all ages and subadult males. Single animals are almost invariably mature bulls and mature bulls can generally be easily separated from mixed groups since they only associate temporarily with any mixed group. The animals in mixed groups comprise 84 per cent of the total desert-dwelling elephant population.

Figure 15 presents the frequency distribution of mixed-group sizes in the northern Namib Desert between 1980 and 1982. Data from different years are lumped as they were homogeneous ($t = -1,78$; $p > 0,05$; df = 225). The mean mixed-group size was 7,01 ± 4,68.

The mixed-group size frequency (Fig. 15) also shows a hollow curve which illustrates the large feeding aggregations of elephants. Observations on seasonal group sizes (see previous section) also showed that the large feeding aggregations invariably broke up during the dry season into certain minimum sized units. Through the process of individual identification it was established that each of these smaller units always consisted of the same individuals which were constant throughout the study period. They were therefore classified as family units, each of which had its own home range and each of which was always

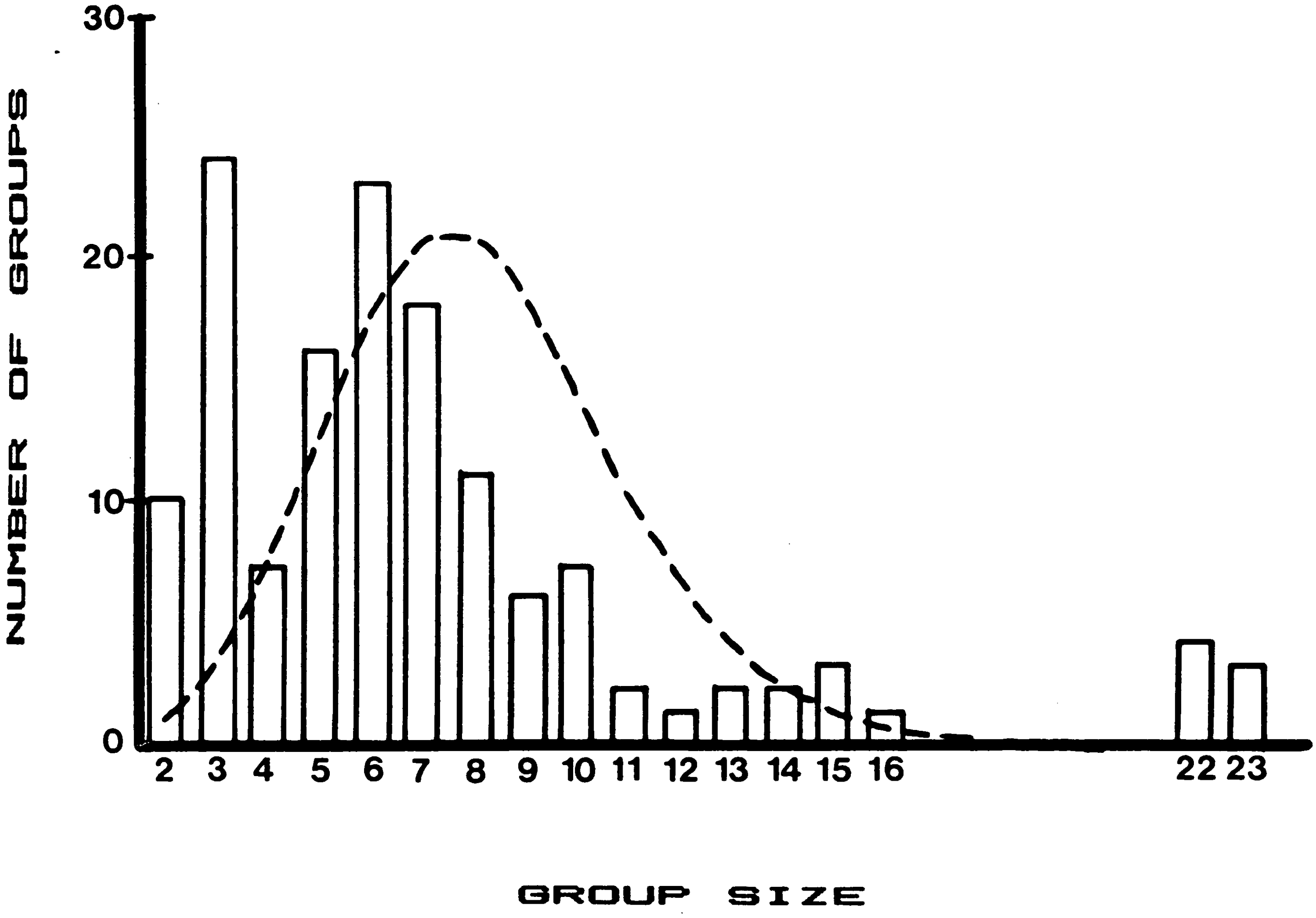


Figure 15: Actual frequency distribution of mixed-group sizes in the desert-dwelling elephant population during 1981 and 1982 in the northern Namib Desert, South West Africa. Expected random group sizes are shown as a Poisson distribution (broken line).

coordinated in terms of movements (Chapter 5). The associations between specific individuals of a unit and the stability thereof were so strong that it was relatively easy to define discrete family units without needing to use any statistical sorting process.

The random expectations for mixed-group sizes are also shown in figure 15 as a Poisson distribution. Obviously, the group sizes were not random ($\chi^2 = 876{,}62$; $p<0{,}001$; $df = 16$), but show a preponderance for groups of three, five and six which correspond with the observed sizes of identified family units. Group sizes other than those of established family units were recorded during systematic aerial and ground surveys when all members of the group were not visible or were spaced 100 or more metres apart, in which case they were reported as separate groups. Due to the nature of the systematic surveys, such cases could not be further investigated. However, during long-term field observations all members of a group could be located and it also showed that although individuals of a group may be up to 200 m apart such a separation seldom lasted more than three hours and thus they were only temporary in nature.

Table 5 depicts the various family units identified within the desert-dwelling elephant population together with a simplified age structure of each family unit. Throughout the study period the family units described in Table 5 remained stable and slight changes in their numbers between 1980 and 1983 were caused by deaths (16), a single birth and two young bulls which apparently

Table 5: Identified family units of the desert-dwelling elephant population in the northern Namib Desert, South West Africa, during 1982.

GROUP REFERENCE NUMBER	GROUP SIZE	AGE STRUCTURE				
		Adult	Subadult	Immature	Juvenile	Calf
OC1	3	1	2			
HH1	10	3	1	5	1	
HH2	6	3		3		
HH3	5	2	3			
HH4	5	2	1	2		
WH1	8	3	3	1	1	
WH2	9	6		1	2	
WH3	7	3	2		2	
KH1	6	4	2			

were in the process of leaving their family units to join the bull groups. Apart from the abovementioned changes the stability of each family unit in terms of structure, movement coordination and home range, remained predictably stable over a period of three years.

These family units consisted of cows and calves of all ages and young male elephants. Young male elephants up to the age of 17 years were permanently attached to a specific family unit. On only two occasions were two young males, aged nine and 17 years old, observed more than 1 km away from their family unit. However, this separation lasted less than a day and they soon rejoined their original family unit.

Table 6 depicts the percentage association of older male elephants with the various family units. From this table it can be seen that although young bulls between 19 and 22 years of age (YB1 and YB2) spend most of their time outside mixed groups (63 per cent of the time), when they do occur in mixed groups, individual young bulls tend to associate with a specific family unit, namely HH1 and HH2. In the case of young bull YB2 and family unit HH2 this association was statistically significant ($\chi^2 = 4{,}32$; $p<0{,}05$; df = 1). These young bulls presumably associated with the family units from which they originated and they were classified as young bulls in the process of leaving the family unit and were not considered as stable members of a specific family unit.

Table 6: Associations between adult bulls and family units in the desert-dwelling elephant population of the northern Namib Desert, South West Africa, from 1980 to 1983.

BULL REFERENCE NUMBER	AGE OF BULL (YEARS)	PERCENTAGE TIME SPENT ALONE	PERCENTAGE TIME SPENT WITH OTHER BULLS	PERCENTAGE TIME ASSOCIATED WITH FAMILY UNITS LISTED BELOW								
				OC1	HH1	HH2	HH3	HH4	WH1	WH2	WH3	KH1
YB1	19	12,2	46,3	4,2	17,1	7,3	7,3	4,9	0,0	0,0	0,0	0,0
YB2	22	13,5	43,2	2,7	8,1	21,6	8,1	2,7	0,0	0,0	0,0	0,0
HB1	45+	11,5	14,8	21,3	14,8	14,8	14,8	4,9	0,0	0,0	0,0	3,3
EB1	45	22,7	47,7	2,3	6,8	9,1	4,5	4,5	2,3	0,0	0,0	0,0
RB1	26	28,6	41,1	3,8	3,8	3,8	3,8	5,8	1,9	1,9	0,0	0,0
LB1	37	25,0	54,2	4,2	4,2	8,3	0,0	4,2	0,0	0,0	0,0	0,0
SB1	28	14,3	62,9	0,0	5,7	8,6	5,7	2,9	0,0	0,0	0,0	0,0

Mature adult bulls over the age of 22 years only temporary joined family units (Table 6), and with one exception did not show a significant association with any one family unit (χ^2 = 0,003 to 2,97; $p>0,05$; df = 1). The exception was adult bull HB1 associated with family unit OC1 (χ^2 = 4,39; $p<0,05$; df = 1) but these latter elephants occupied a dry season range where no other elephants occurred and with a limited distribution of food and water. Therefore, their apparent affinity to each other could have been more a function of the distribution of food and water, rather than a social function.

Family units seemed to be a classical case of a mother-offspring relationships (Laws 1970, Douglas-Hamilton 1972). In some family units relationships were clear, such as cows with suckling calves or cows with juveniles which constantly remained at their sides. Other family relationships remain presumptive although it would be reasonable to assume that immature and subadult elephants would remain with their mothers and therefore inside the same family unit. The pattern of the age structure in some family units is very suggestive (Table 5) where family units usually consist of older females (matriarchs) and younger animals of all ages and they therefore could well be related to each other. However, in some family units (WH1, OC1, HH3, HH4), it appeared as if one or more matriarchs were missing, presumably having been killed as 31 per cent of the elephant carcasses aged were of females older than 30 years which could possibly have been matriarchs. For example, in family unit OC1, all the members of the family unit were approximately of the same age (Table 5) and could therefore not be a classical case of a mother-offspring relationship. This latter group in fact represents the sole survivors of a formerly much larger group which was nearly exterminated in a poaching spree in 1978.

Some of the larger family units, such as HH1, WH1 and WH2, tend to split into subgroups, each group always consisting of the same individuals. This separation into subgroups, however, was only temporary and the groups always remained in the same vicinity. It might be that they were in the process of forming new family units but during the study period the subgroups of each respective family unit were clearly integrated, cohesive and stable and up to 1983 at least could only be classified as an extended family unit according to Douglas-Hamilton (1972).

Association between family units

During the wet season, there appeared to be a tendency for specific elephant family units of the desert-dwelling population, to clump into separate feeding aggregations which were associated with a certain geographical range, suggesting that there may be an intermediate level of organization between different family units, and also between family units and bulls (Table 6). A similar level of organization is known to apply to elephant populations elsewhere (Martin 1978, Moss and Poole 1983, Hall-Martin 1987) and is defined as bond groups or clans which typically consist of several family units and bulls which occupy a largely exclusive range.

Figure 16 is a visual representation of the percentage of observations that each family unit was observed in the company of another family unit. Although only three associations, namely that between HH1 and HH2, WH1 and WH2 and WH2 and WH3, appear to be greater than could be expected randomly (χ^2 = 5,48, 31,18 and 12,67 respectively; $p<0,05$; df = 1), a pattern emerged when the degree of contact or rather lack of contact between various family units is studied. There were frequent contacts between family units OC1, HH1, HH2, HH3 and HH4 in the Hoanib River area, while family units WH1, WH2 and WH3 formed a separate group in the Wêreldsend area. Between these two groups of family units there were very little contact. Similarly, family unit KH1 made limited contact with OC1 and none with the other family units. These separate congregations might well represent different clans. Also certain bulls showed a tendency to contact family units of a certain clan (Table 6) although there generally was no positive association of a given bull with a given family unit except in the case of younger bulls between 19 and 22 years of age.

Bull groups

Only bulls older than 17 years which were not permanently associated with a family unit, were used in the calculations. Adult bulls comprised 16 per cent of the total desert-dwelling

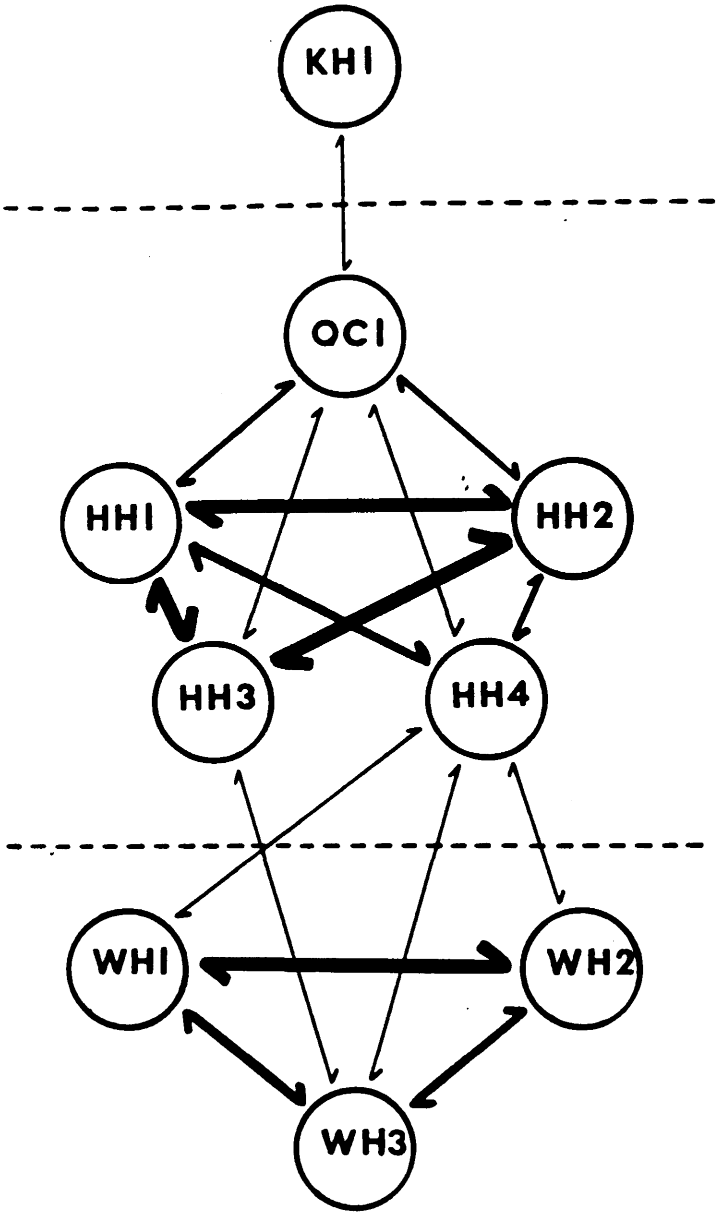
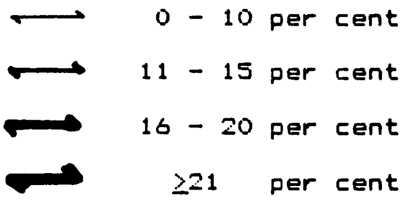


Figure 16: Family unit associations, depicting possible clans, in the desert-dwelling elephant population of the northern Namib Desert, South West Africa, between 1980 and 1983. Circles indicate identified family units and broken lines demarcate possible clans. Line thickness indicates percentage association between two family units.



elephant population. In 213 observations of bulls, 28 per cent were accompanied by mixed groups, 27 per cent were single bulls while 45 per cent occurred in bull groups ranging from two to seven animals in size. Single elephants observed in the northern Namib Desert were almost invariably bulls as 97 per cent of the single animals were bulls and the rest (3 per cent) could not be classified during aerial surveys. Of the elephants found in pairs, 70 per cent were bulls, 20 per cent of unknown sex and 10 per cent were either two cows or a cow and an calf.

The seasonal frequency distribution of bull-group sizes between September 1980 and January 1983 is represented in Figure 17. Although seasonal differences are not statistically significant ($F = 1{,}184$; $p > 0{,}05$; $df_1 = 2$, $df_2 = 93$), possibly as a result of the low numbers of the bulls, it is consistent with the trend found in seasonal social organization and might well be biologically meaningful. The mean elephant bull-group size for the wet season was 1,33 ±,05, compared to that of the cold dry season with a mean of 1,89 ±0,99 and the hot dry season mean of 1,55 ±0,99. In the wet season bulls occurred singly or in pairs while larger groups were absent. In both the dry seasons the bulls tend to be more gregarious with 21 per cent in the cold dry season and 27 per cent in the hot dry season occurring in groups larger than two.

In neither the wet nor the hot dry season were the bulls grouped randomly ($\chi^2 = 17{,}38$ and $42{,}91$; $p < 0{,}05$; $df = 5$), but in the cold dry season the bull grouping was not significantly different from

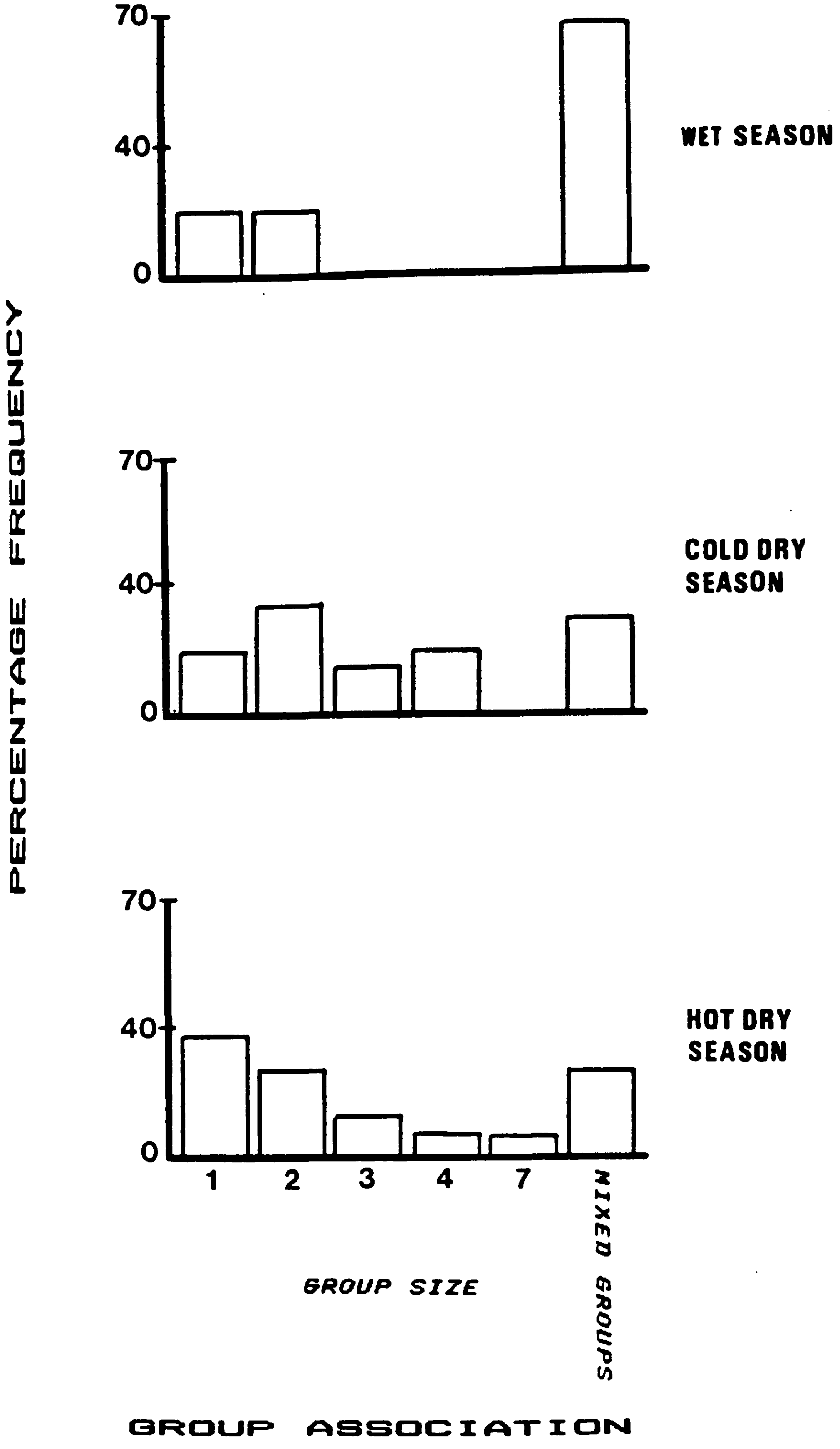


Figure 17: Seasonal frequency distribution of bull group sizes and percentage bulls occurring in mixed groups in the desert-dwelling elephant population during 1981 and 1982 in the northern Namib Desert, South West Africa.

random (χ^2 = 6,57; p>0,05; df = 5). In the wet season there was a preponderance of bulls in mixed groups while in the hot dry season there was a preponderance of single animals and groups larger than four.

Table 7 depicts the seasonal social organization of bulls older than 17 years in terms of the percentage of bulls associated with a specific group in the desert-dwelling elephant population. In the wet season, presumably the most competitive time of the year when conceptions and hence matings were more frequent, most bulls were associated with mixed groups while associations with other bulls were low. Thereafter there was a decrease in the number of adult bulls in mixed groups with a corresponding increase in bull groups. During the hot dry season a larger proportion of the bulls occurred singly.

Bull associations

Bull groups appear to be unstable in the northern Namib Desert and their numbers and composition fluctuated frequently, sometimes several times in a 24-hour period. For example, one bull, identified as RB1, was tracked for a period of 14 days. During that time he spent eight days alone and during the remaining six days he associated with four different bulls and two different family units on ten separate occasions. Only four of the observed associations between bulls lasted unbroken for more than seven days.

Table 7: Seasonal variation in the social organization of adult elephant bulls in the desert-dwelling elephant population of the northern Namib Desert, South West Africa, between 1980 and 1983.

SEASON	SAMPLE SIZE	PERCENTAGE SINGLE BULLS	PERCENTAGE OF BULLS IN PAIRS	PERCENTAGE OF BULLS IN GROUPS > 2	PERCENTAGE OF BULLS IN GROUPS OF MIXED SEX
Wet	48	16,7	16,7	0,0	66,7
Cold Dry	96	16,7	29,2	29,2	25,0
Hot Dry	141	32,6	24,1	21,3	22,0

The identity of 14 of the adult bulls older than 17 years in the northern Namib Desert, and the number of times that they were observed in the company of each other are shown in Table 8. Five of the bulls died between 1981 and 1982 but for the sake of comparison, they are also included in the table. Positive associations between two bulls depend on the frequency of joint occurrences relative to the number of times that each was observed independent of the other (Croze 1974a). All the joint occurrences in Table 8 were tested for significance by the chi-square test using a 2 x 2 contingency table. Only three were greater than could be expected proportionally: Between bulls SB1 and RB1 ($\chi^2 = 6{,}73$; $p<0{,}01$; df = 1), OB1 and LB1 ($\chi^2 = 17{,}83$; $p<0{,}001$; df = 1) and between YB1 and YB2 ($\chi^2 = 9{,}00$; $p<0{,}01$; df = 1).

Bulls YB1 and YB2 were both young bulls (aged 19 and 22 years), who also showed a positive association with specific family units, and they appeared to be young bulls in the process of leaving their respective family units. Being compatriots in the sense that they are both young and apparently not fully integrated in the mature bull society, they seemed to seek the company of each other. The association between OB1 and LB1 might not be meaningful because it represents observations over a relatively short period of time (12 months) as OB1 was shot early in 1982. Therefore, the only apparent positive association between older adult bulls were those of SB1 and RB1. However, with the low number of adult bulls available in the northern

Table 8: Association matrix of the number of times that adult bulls from the desert-dwelling elephant population in the northern Namib Desert, South West Africa, were seen in the company of each other between 1980 and 1983. The three significant associations are indicated in parantheses.

BULL REFERENCE NUMBER	HB1	EB1	NB1	SB1	BB1	RB1	GB1	B6	B9	OB1	HU1	LB1	YB1
EB1	1												
NB1	1	1											
SB1	1	1	4										
BB1	1	1	1	2									
RB1	1	1	4	(6)	2								
GB1	0	1	0	2	1	2							
B6	1	0	1	1	1	1	0						
B9	0	1	0	1	1	1	1	1					
OB1	1	2	2	1	1	1	0	1	0				
HU1	0	2	0	1	1	1	1	0	1	1			
LB1	0	2	1	0	0	0	0	0	0	(4)	1		
YB1	1	4	1	2	0	1	0	0	0	1	0	1	
YB2	0	2	1	1	0	1	0	1	0	1	0	1	(5)

BULL REFERENCE NUMBER

Namib Desert this means that the chance of association between any two bulls is higher than in those populations with a high number of adult bulls. Thus it might well be that SB1 and RB1, which frequent the same geographical range, were together more by chance of intraspecific encounters than by individual choice.

AGE STRUCTURE

Mortality and molar age structure

Between 1980 and 1982, 123 elephant carcasses were found in the Kaokoveld. The distribution of these carcasses is shown in Figure 18. Of the carcasses found, 94 could be aged by using the mandibles, the remainder being unsuitable for ageing due to the burning of carcasses or of mandibles being lost due to predators or other factors. Of the mandibles that could be aged according to Laws' (1966) technique, 34 were found in the northern Namibian Desert and classified as being from the desert-dwelling elephant population, 40 belonged to the transitional elephant population and 20 from the eastern elephant population.

Of the aged mandibles 71 per cent of the desert-dwelling elephant population, 98 per cent of the transitional and 65 per cent of the eastern population were from elephants that positively had been shot, either through illegal hunting or through a trophy hunting concession. In addition, a further two elephants were killed by other human interferences. The cause of death of 13

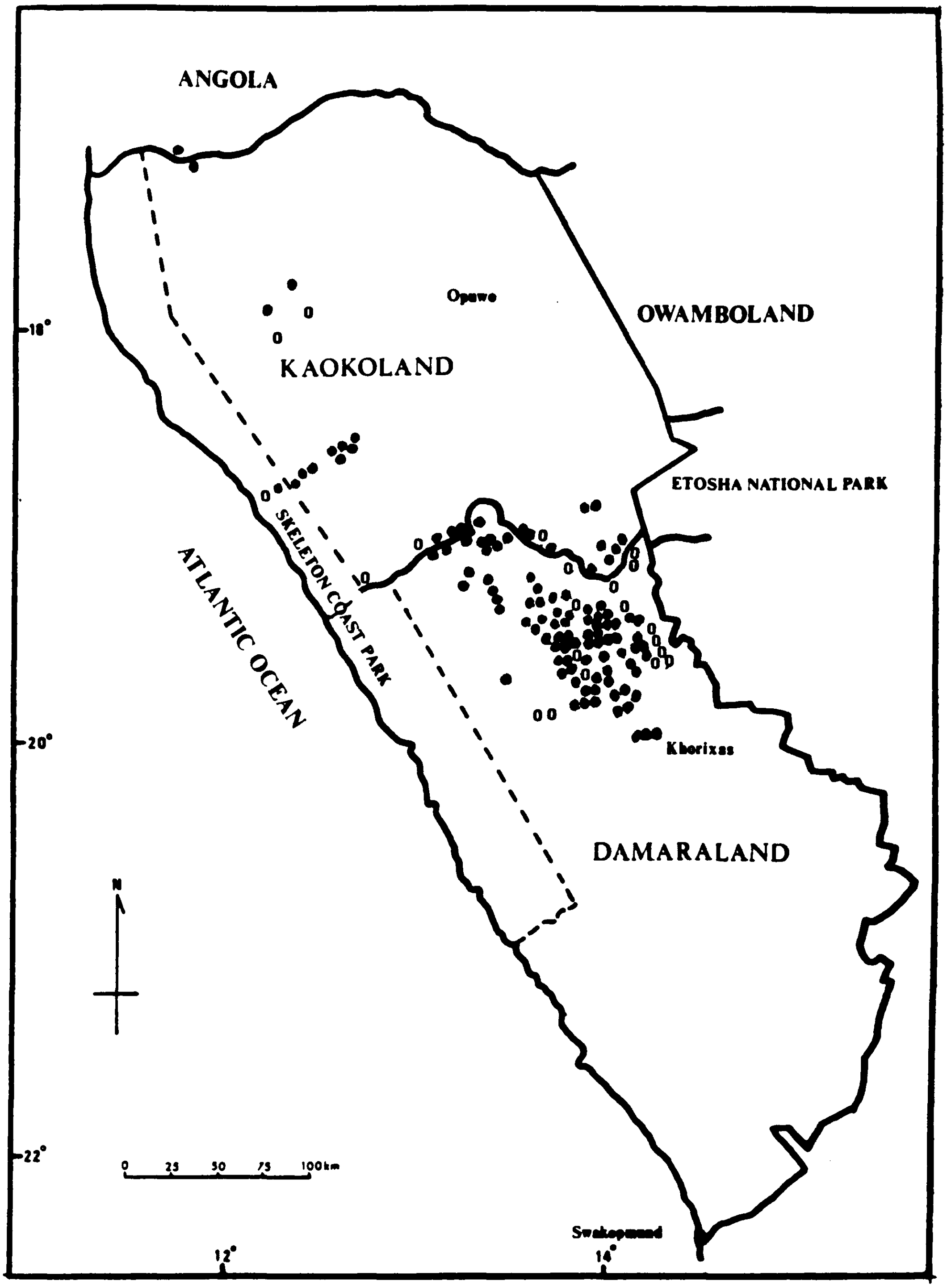


Figure 18: Known distribution of carcasses of elephants which died between 1979 and 1982 in the Kaokoveld, South West Africa. ● indicate elephants that were shot and 0 elephants that died from other causes.

elephants is unknown but the possibility cannot be ruled out that they died from gutshot wounds. Only six elephants were thought to have died naturally, five being from the eastern elephant population that probably died as a result of the drought and one 57-year old cow of the desert-dwelling population, that probably died of old age.

Thus a minimum of 83 per cent of the mandibles aged in Table 9 is not representative of the natural mortality of the elephants in the Kaokoveld. Neither can it be regarded as a random sample as both poachers and trophy hunters would tend to select older elephants for their tusks, as is indicated by the large percentage (51 per cent) of animals older than 25 years that were shot. In some incidences, however, entire family groups were shot by poachers.

Thus, it would not be valid to draw any inferences from the age composition of the carcasses found in the field. It can only be regarded as a non random sample of the living elephant populations and as such it can only be used in conjunction with the observed age structure of the living populations. Therefore, the allotted ages based on found mandibles from the desert-dwelling elephant population are combined with those of the living elephants to construct meaningful natural age structures and inferences about the reproductive strategies of the desert-dwelling population and the environmental influences thereon.

Table 9: Molar age classification of Laws (1966) on elephant carcasses found between 1980 and 1982 in the Kaokoveld, South West Africa, adjusted to the base year 1982.

AGE CATEGORY OF LAWS (1966)	ESTIMATED AGE IN YEARS	ELEPHANT POPULATION					
		Desert-dwelling		Transitional		Eastern	
		n	%	n	%	n	%
1V	2	1	2,9	0	0	1	5,0
V1	4	3	8,8	6	17,5	2	10,0
V11	6	0	0	2	5,0	1	5,0
V111	8	1	2,9	3	7,5	0	0
1X	10	0	0	1	2,5	1	5,0
X	13	1	2,9	3	7,5	0	0
X1	15	2	5,9	8	17,5	4	20,0
X11	18	1	2,9	1	2,5	1	5,0
X111	20	0	0	2	5,0	0	0
X1V	22	0	0	0	0	1	5,0
XV1	26	2	5,9	1	2,5	0	0
XV11	28	1	2,9	2	5,0	0	0
XV111	30	3	8,8	2	5,0	1	5,0
X1X	32	3	8,8	0	0	2	10,0
XX	34	2	5,9	0	0	1	5,0
XX1	36	6	17,6	3	7,5	0	0
XX11	39	3	8,8	3	7,5	3	15,0
XX111	43	0	0	1	2,5	0	0
XX1V	45	1	2,9	1	2,5	0	0
XXV1	49	0	0	0	0	1	5,0
XXV11	53	2	5,9	0	0	0	0
XXV111	55	0	0	1	2,5	1	5,0
XX1X	57	2	5,9	0	0	0	0

Age structure of the living elephants.

The shoulder height of 64 of the 70 desert-dwelling elephants still alive in 1982 were obtained by the pole measuring method as previously described. The next step was to relate the height measurements to meaningful age categories which will be compatible with the allocated molar ages of the elephant carcasses, in order to construct the natural overall age structure of the desert-dwelling elephant population in the absence of human induced mortality.

While it is generally accepted that assigned molar age categories remain constant for all elephant populations in Africa (Fatti _et al_. 1980, Lark 1984, Jachmann 1985) , it is not necessarily the case in the growth rate of individuals of different populations. Croze (1972), Douglas-Hamilton (1972) and Laws _et al_. (1975) are of the opinion that there is only a slight variation between the growth rates of individuals in different populations and that local differences would only slightly affect age estimates. However, the work of Hanks (1972a), Malpas (1977) and Jachmann (1986) showed that there is differences in individual growth rate and therefore in shoulder-height:age relationships between different populations in different regions and also between wild and captive elephants. This would influence the resultant age structures when using the shoulder-height:age calculations derived from assigned molar age categories of other populations. It would therefore be invalid to assume that the growth rate of elephants from populations in East Africa or Zambia could be applied to that of the elephants in the northern Namib Desert in the south-west of Africa. Fortunately, the shoulder heights of three female elephants from the desert-dwelling elephant population could be measured and their molar ages estimated independently, following the method of Laws (1966), making comparisons of the age:height relationships possible with that of other populations.

Laws _et al_. (1975) and Hanks (1972a) assessed the growth of elephants by using the Von Bertalanffy (_In_ Hanks 1972a) growth equation. As Hanks (1972a) explained, however, this equation is empirical and there is little biological significance in the parameters. Hanks (1972a) further suggests using the regression of Log_{10}age on Log_{10}shoulder-height in comparative growth studies. The latter approach was adopted in this study to construct age-height relationships of the female desert-dwelling elephants.

The regression of Log_{10}age on Log_{10}shoulder height for female elephants (n=3) in the northern Namib Desert has a correlation coefficient of 0,985 and the equation describing the height-age relationship is:

Log_{10}shoulder height = Log_{10}age 0,173 + 2,131 cm.

The shoulder height-age relationship of female elephants measured in Zambia (Hanks 1972a) is described as Log_{10}shoulder height = Log_{10}age 5.31 + 11,03 cm. For the growth rate of the east African elephants, the original Von Bertalanffy equation where Ht = 252 1 - exp < -0,099 (t + 6,00)> cm of Laws _et al_. (1975) has been used since the raw data is not available to convert it to the regression of Log_{10}age on Log_{10}shoulder height.

Figure 19 shows the actual growth curve for the shoulder height of female elephants in the desert-dwelling elephant population, together with the growth curves of elephants from Zambia (Hanks 1972a) and East Africa (Laws et al. 1975) each derived from the formules previously described. From this figure it is clear that while the shoulder height at a given age of the Zambian elephants is generally lower than that of the other two populations, there is a high degree of overlap in the height-age curves of the desert-dwelling elephants and those of East Africa. The discrepancy between the growth rate of East African elephants and that of the northern Namib Desert elephants (in females older than 40 years) might be attributed to the small sample size (n = 3) of the present study and the one measurement of probably an exceptionally large 57-year old female elephant.

To test whether the growth:molar age relationship of the female elephants in the northern Namib Desert is similar to that of other populations, age structures derived from the shoulder height measurements obtained during this study were constructed using each of the above formulae. Using a chi-square test and by treating the age structures derived from the shoulder height:age relationship of the East African and Zambian elephants as expected age structures, there was no significant differences between the resultant age structure derived for the desert-dwelling elephants and that of East Africa ($\chi^2 = 20,48$; $p>0,05$; df = 37). However, between the northern Namib Desert elephants and that of Zambia, the differences in the assigned age structure was significant ($\chi^2 = 113,87$; $p<0,001$; df = 37).

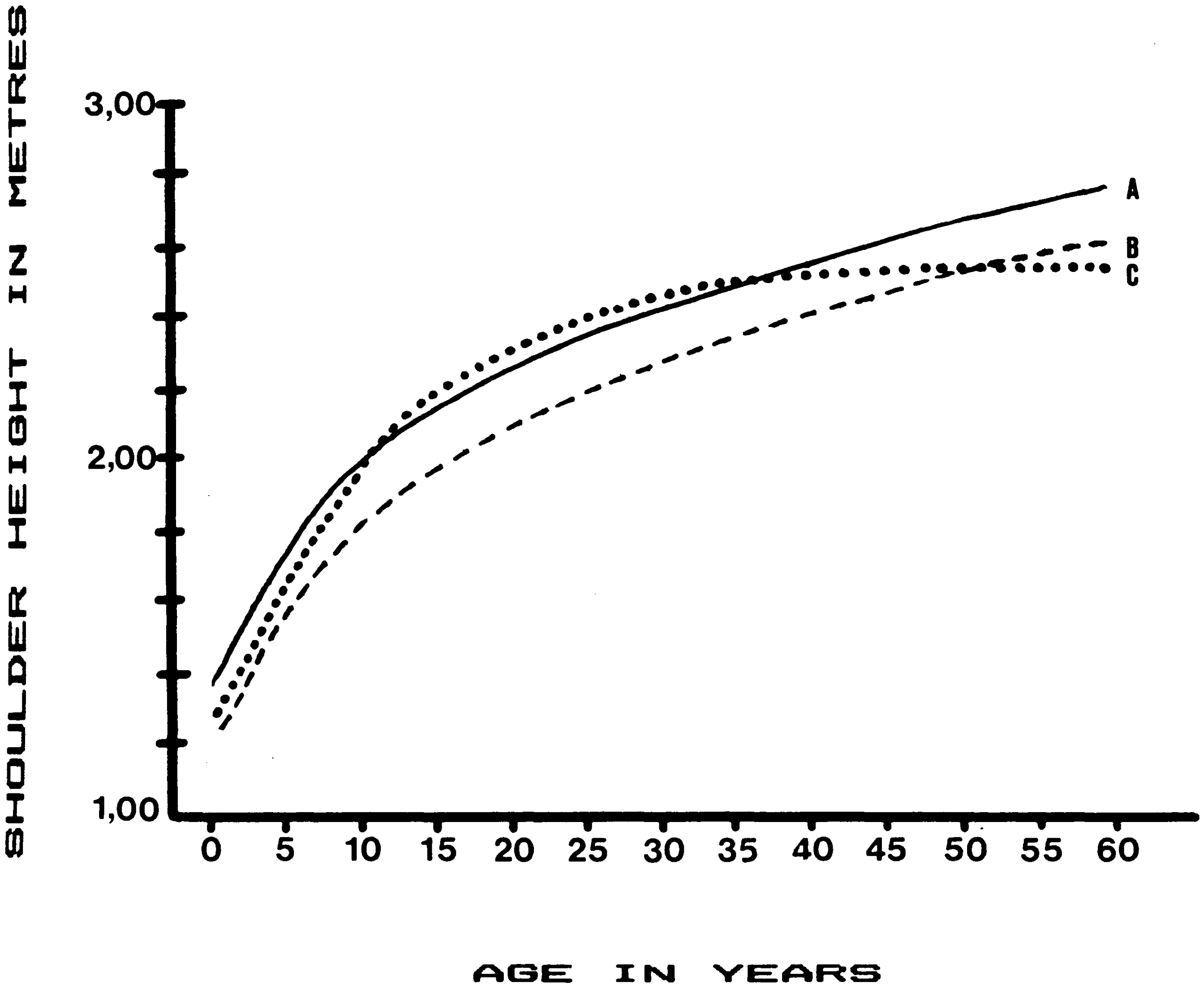


Figure 19: Relationship between shoulder height and age in the female African elephant in (A) the northern Namib Desert, (B) Zambia (Hanks 1972a) and (C) East Africa (Laws <u>et al</u>. 1975).

It would therefore appear that the shoulder height:molar age relationships of the female desert-dwelling elephants is similar to that of East Africa and that it might be valid to combine the age structures of elephants derived from the height measurements with that derived from the molar ageing technique of Laws (1966). However, because of the small sample size available from the present study, such a resultant age structure must be approached with caution.

Laws _et al_.(1975) illustrated differences between the growth rate of male and female elephants, especially after the male's post-pubertal growth spurt. The growth rate of the female can therefore not be used alone for constructing the age structure of the desert-dwelling elephant population. No data are available on the growth rate of male elephants in the northern Namib Desert. However, since there seems to be no significant differences between the growth rate of female elephants of the northern Namib Desert and that of East Africa, the equation for the growth rate of male elephants of Laws _et al_. (1975) is used in this study to construct an approximate the age structure of the desert-dwelling male elephants.

Figure 20 depicts the approximate age structure of the living desert-dwelling elephant population during the base year 1982. The ages of females were constructed from the shoulder-height:age relationships obtained during this study and the ages of male

Figure 20: Approximated age structure of the living desert-dwelling elephant population (n = 64) during the base year 1982 in the northern Namib Desert, South West Africa, based upon shoulder-height:age relationships as discussed in the text. The frequencies for the composite age-classes, 11-28, 29-44 and 44+ have been divided by 2, 4 and 16 respectively, to make them consistent with the frequency of the 1-10 year-old classes (see text).

elephants from the height:age data of Laws et al. (1975). Age classes were allocated according to the amount of growth between successive years. The smaller the difference in growth between successive years, the greater the possibility of erroneous age allocation. Between ages of 1 - 10 years, there is a yearly growth increment of at least 40 mm in shoulder height between successive years. Between ages 11 to 24 years the increment is approximately 30 mm per year, between 25 to 44 years of age the increment is 20 mm and in elephants older than 44 years the yearly increment of growth is less than 10 mm. Age class intervals were therefore allocated accordingly.

The original data on the age distribution of the desert-dwelling elephant population were obtained during the base year 1982. However, the yearly calving increment between 1983 and 1986 is also known (S.Brain pers. comm. 1986). No mortality in the desert-dwelling elephant population was reported between 1983 and 1986 (S.Brain pers. comm. 1986, Owen-Smith 1986) and with an increase in rainfall and law enforcement measures, it is assumed that there was little or no mortality in the older age classes. Consequently, the approximate age distribution of the elephants as in 1982 (Fig. 20) was adjusted to construct a more recent representation of the age distribution of the living desert-dwelling elephant population as in 1986 (Fig. 21).

S.Brain, Skeleton Coast Park, P/bag 5001, Swakopmund, S.W.A.

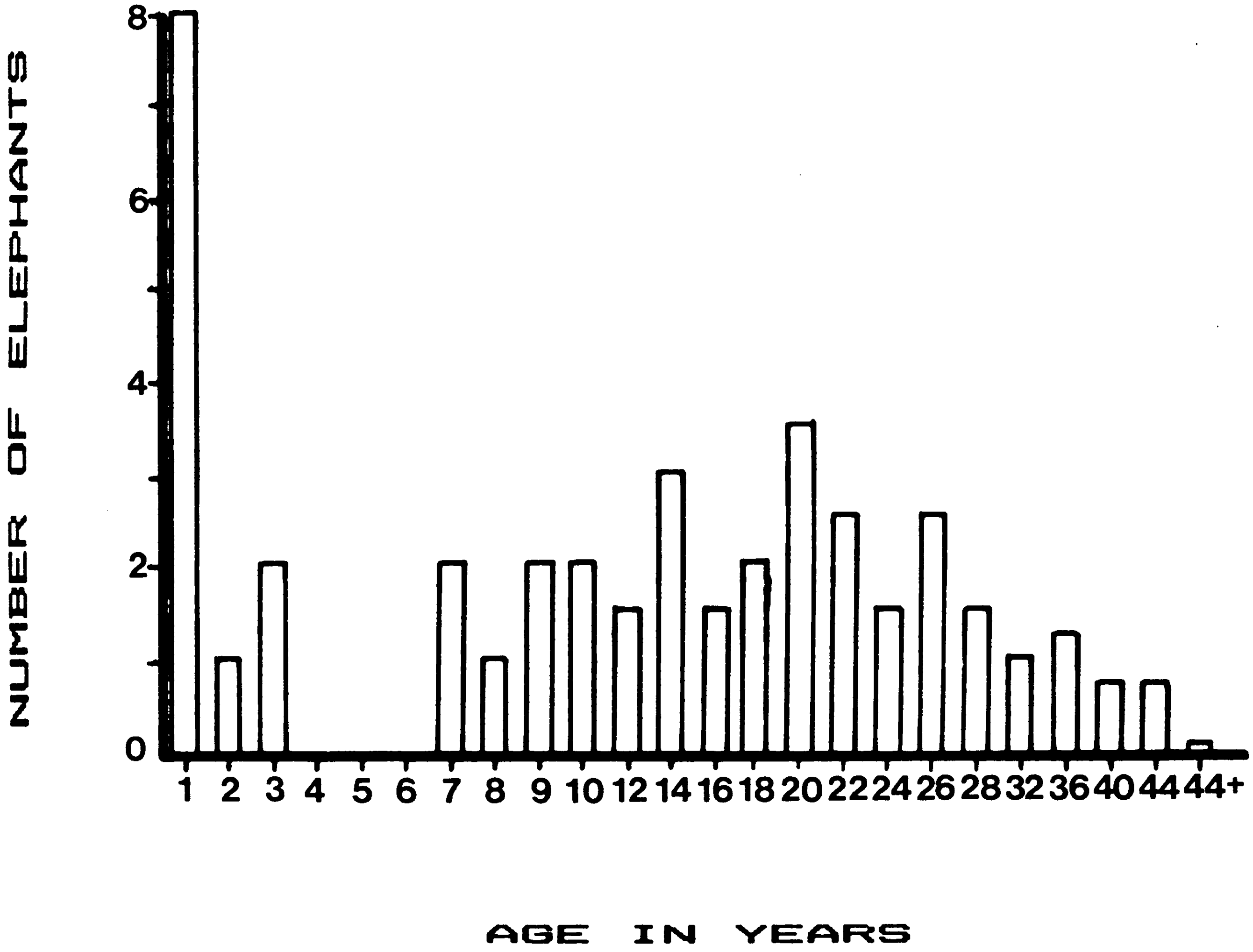


Figure 21: Adjusted age structure representing the living desert-dwelling elephant population (n=75) in 1986 in the northern Namib Desert, South West Africa. Incorporating the adjusted ages of the elephants alive in 1982 as well as the ages of additional calves (n=11) born between 1983 and 1986. The frequencies for the composite age-classes, 11-28, 29-44 and 44+ have been divided by 2, 4 and 16 respectively, to make them consistent with the frequency of the 1-10 year-old classes.

However, as mentioned earlier, the age structure of the living elephants as shown in Figures 20 and 21, is not representative of the natural age structure of the desert-dwelling elephant population, and the latter will be analysed in conjunction with the ages of found elephants carcasses in the following section.

Combined age distribution

A histogram showing the combined adjusted age class frequencies during 1986 of both the living elephants and those derived from mandibles of shot elephants appears in Figure 22 which presumably is more representative of the natural age distribution of the desert-dwelling elephant population. This combined age distribution will not be affected by additional mortalities between 1983 and 1986.

As reflected in the age distribution of the living elephants, the combined age distribution also shows a large variation in age-class sizes, suggesting either a large variation in age-specific mortality rates or in yearly recruitment. It could also be the result of artificially introduced peaks and troughs due to errors in the ageing technique employed (Hanks 1972a, Fatti _et al_. 1980, Jachmann 1985). However, the ages of the calves born between 1980 and 1986 are known from field observations during the year of birth and are therefore accurate. Also, animals up to nine years old in 1986 were probably classified within the correct year age-class, as they were only five years old when first aged in 1982. It is relatively easy to assign year classes

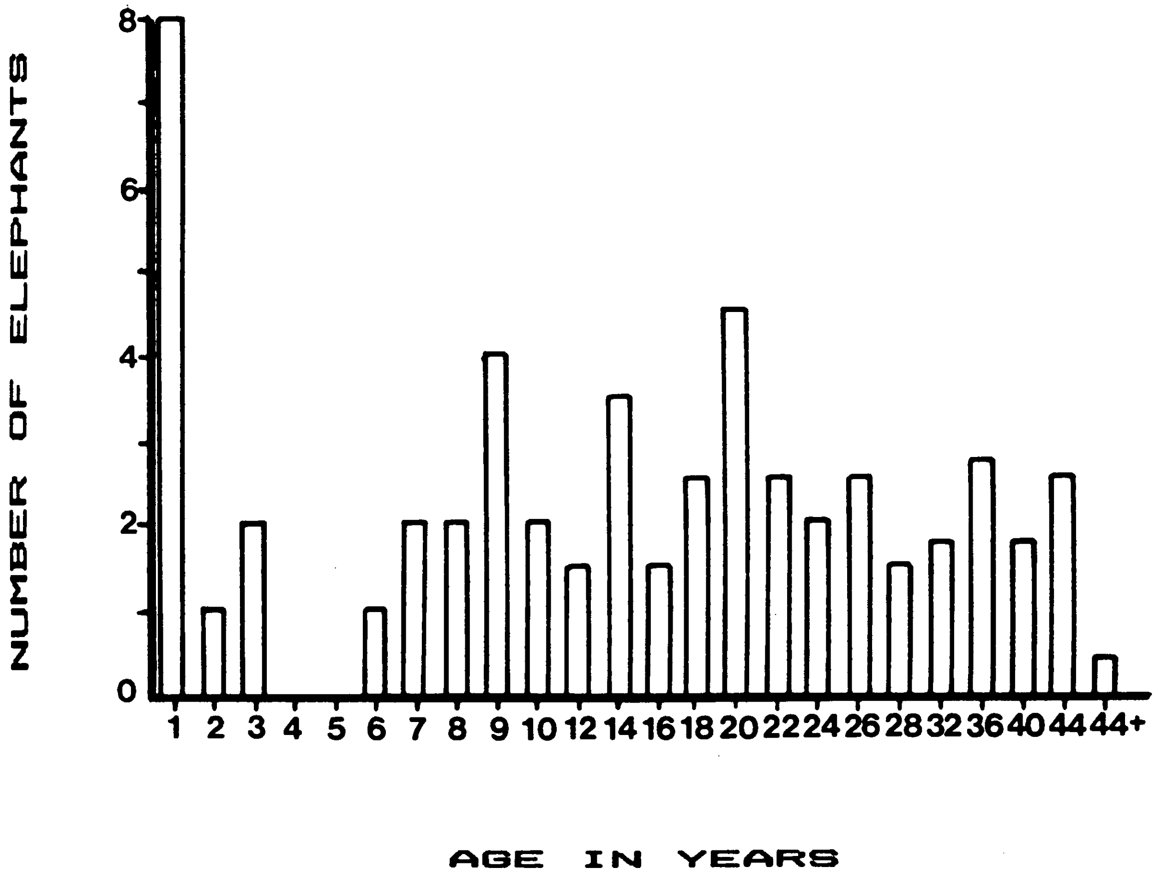


Figure 22: Combined age class frequencies of the desert-dwelling elephant population (n=109) during 1986 in the northern Namib Desert, South West Africa, illustrating the probable natural age distribution as it would be in the absence of human-induced mortality. These data incorporate the ages of the living (n=75) elephants as well as those derived from mandibles (n=34) of shot elephants (see text). The frequencies for the composite age-classes, 11-28, 29-44 and 44+ have been divided by 2, 4 and 16 respectively, to make them consistent with the frequency of the 1-10 year-old classes.

to animals up to five years old, when differences between one year and the next are marked due to rapid growth (Laws 1966). Thus, animals up to nine years old in 1986 are judged to be accurately aged. As the variation in age class sizes is also conspicuous in these younger animals, an artificially introduced variation due to an inaccurate ageing technique can thus probably be ruled out as a possible cause of variation in the age-class structure.

Hunting or poaching might have caused age-specific mortality, but hunters usually select older animals for their tusks. This is evident from the fact that 74 per cent of the shot desert-dwelling elephants were older than 25 years of age. Therefore, mortality due to hunting does not explain the variation in the size classes of the younger ages and therefore probably also not in the older age classes since the age-class variation in the younger age classes will be carried over to the older age classes.

A more feasible explanation might be age-specific mortality introduced by environmental conditions among which rainfall and its influence on the vegetation might be important. Dry year mortality of the youngest and oldest age groups may be greater than in a wet year. Continuous rainfall data for Sesfontein between 1971 and 1984 are available but there was no significant correlation between rainfall and the number of calves surviving during a specific year (r = -0,431; t = -1,655; df = 13; p>0,05), indeed, what correlation there is, is also negative. Thus, rainfall appears to have had little influence on the survival of calves born in a specific year.

Age-specific mortality might also be the result of a higher mortality in newly-weaned animals. Croze (1972) and Jachmann (1980) reasoned that during a severe drought there may be increased deaths among newly-weaned animals who are too short to reach the higher browse in the absence of grass and herbs, and also among very old animals whose teeth may not be able to masticate the coarse vegetation left. To test this theory, the number of elephant calves presumed to be newly weaned in a specific year, were tested for correlation with rainfal during that given year. Since it is unknown at what age elephant calves are weaned in the northern Namib Desert, the number of elephants at either 2, 3 or 4 years of age respectively, were tested separately for a possible correlation with rainfall in a given year. However, no significant correlation could be found between the number of animals presumed to be newly weaned and rainfall during the year that they reached that given age ($r = -0,017$, $0,178$ and $-0,318$ respectively; $t = -0,058$, $0,628$ and $-1,161$; $p > 0,05$; df = 13). Thus a higher mortality in newly weaned elephant calves can probably also be ruled out as a possible cause of a variation in the age-class structure.

The apparent lack of age-specific mortality caused by environmental conditions is puzzling; the population will be unique if this were not true. However, as pointed out earlier, most of the mortality, at least between 1979 and 1982, was artificially caused by poaching. The high incidence of poaching might, in a way, have prevented natural deaths in the population by killing animals that might have otherwise have died naturally. Alternatively, it kept the population at such a low level that the population stayed within the carrying capacity of the region to the advantage of the survival of the remaining elephants even at times of severe drought.

While the data do not seem to support the occurrence of a clear age-specific mortality, the variation in age-class sizes appears to be a function of recruitment rate. By comparing the year of conception of the age-class sizes of the population since 1971 with the rainfall (Fig. 23) a significant positive correlation emerged ($r = 0{,}749$; $t = 3{,}921$; $p<0{,}01$; $df = 13$). This is evident in Figure 23 where the high frequency found in the one year age-class of 1986 corresponds to a relatively large amount of rainfall during 1984, the year in which the calves were conceived (gestation = 22 months). The dip of two year old animals which were born in 1985 is related to the relatively low rainfall of 1983. The lack of calves during 1983 and 1982 corresponds to the extremely low rainfall or lack of rain during 1980 and 1981. In fact, at least since 1971, natality is clearly related to the amount of rainfall recorded during the year of conception.

SEX DETERMINATION OF ELEPHANT MANDIBLES

The widths of 19 mandibles from elephants of known sex in the desert-dwelling and transitional elephant populations were

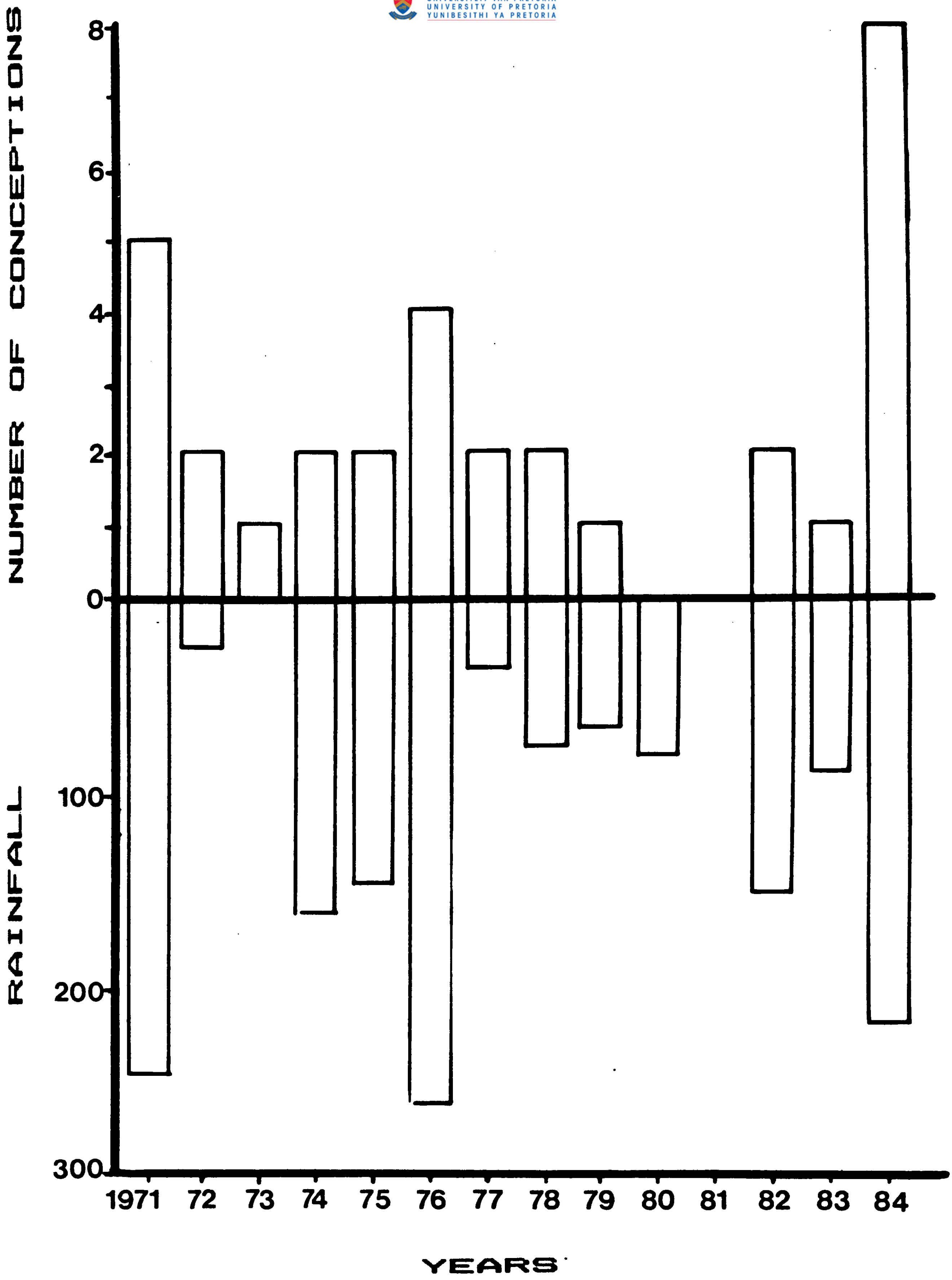


Figure 23: Comparison between year of conception of elephant calves in the desert-dwelling elephant population and rainfall (mm) in the northern Namib Desert, South West Africa.

plotted against age for male and female elephants separately and the relationships were tested. The relationship between these variables is best expressed in terms of common logarithmic functions. It is immediately apparent from Figure 24 that mandible width and age are closely related but differently so for each sex. The linear correlation coefficient between mandible width and age for females is 0,938 ($t = 7,676$; $p<0,01$; $df = 9$) and for males it is 0,965 ($t = 10,476$; $p<0,01$; $df = 8$), both of which are significant. There is also a significant difference between the sexes in the slope of the relevant regression lines ($F = 6,554$; $p<0,01$; $df_1 = 1$, $df_2 = 17$).

The standard deviation of the regression for male elephant mandibles in the northern Namib Desert is ±20,95 mm and for females is ±18,36 mm. Consequently there is little overlap between the sexes in the higher age classes ($\geq$ 15 years). In the lower age classes (<15 years), the growth rate of male and female elephant is similar (Laws et al. 1975). Also no mandible from reliably sexed elephants under the age of 15 years were available for measurement in this study. Yet, for older unsexed carcasses, the width at a given age of the mandibles can therefore serve as a useful tool in the field to determine the sex. In practice, the mandibles ($\geq$ 15 years), examined clearly fell into one of the two sex categories. Also the largest mandible measured in a 57-year old female elephant was 440 mm wide, a width already reached at 32 years of age in the male elephant. Therefore, mandibles notably wider than 440 mm, can safely be assumed to be those of male elephants.

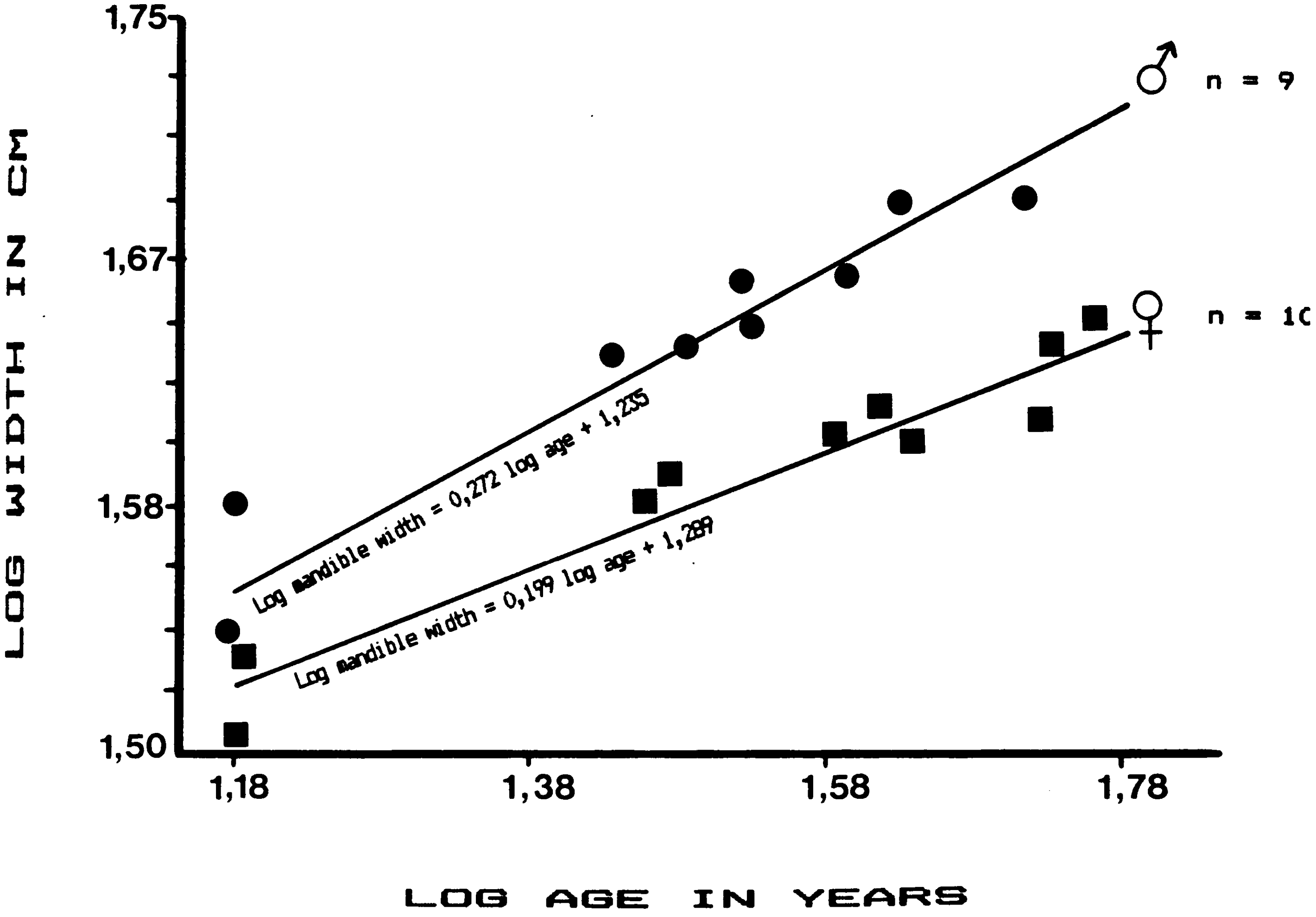


Figure 24: Regression of log mandible width on log age for 15 to 60-year old male and female elephants in the northern Namib Desert, South West Africa.

SEX RATIO

All the desert-dwelling elephants alive in 1982 and 25 of the carcasses found could be sexed either visually or by the mandible width method. The remainder of the carcasses could not be sexed, either because the above measurement could not be taken (mandible halves separated) or because the elephant carcasses involved were too young (<15 years old) to sex reliably. The sexes of calves born after 1983 are unknown and are not incorporated in the 1982 base year.

The overall sex ratio of the living population in 1982 was 1 male:1,69 females (26♂♂ : 44♀♀) which is significantly different from a 1:1 ratio ($\chi^2 = 4,63$; $p<0,05$; df = 1). Following the division of other workers (Croze 1972, Hanks 1972b, Corfield 1973, Smuts 1975, Kerr 1978, Jachmann 1986) the sex ratio for animals younger than 15 years of age was calculated separately. This gives a sex ratio of 1 male:1,43 females (14♂♂ :20♀♀) for young elephants (<15 years) which is not significantly different from a 1:1 ratio ($\chi^2 = 1,06$; $p>0,05$; df = 1). In animals 15 years and older, the sex ratio was 1 male:2,0 females (12♂♂ :24♀♀) which is significantly different from unity ($\chi^2 = 4,00$; $p<0,05$; df = 1).

The oldest bull classified as being a permanent member of a family unit was 17 years old. The sex ratio of animals from family groups which include all females in the population as well as males up to the age of 17 years was 1 male:2,93 females (15♂♂:44♀♀) which is highly significantly different from a 1:1 ratio (χ^2 = 14,25; $p<0{,}001$; df = 1).

As mentioned earlier, sex differentiation in carcasses found in the field is only valid for animals from 15 years upwards of age. When the sexes of these elephant carcasses (≥ 15 years of age) are incorporated with those of the post-14 year old live population, a sex ratio of 1 male:1,85 females (20♂♂:37♀♀) was found which again is significantly different from unity (χ^2 = 5,07; $p<0{,}05$; df = 1).

AGE AT SEXUAL MATURITY AND CALVING INTERVAL

During 1982, four females in the desert-dwelling elephant population were, with reasonable certainty, judged to have had only one calf to date. These females were aged 28, 26, 22 and 19 years old and were accompanied by calves aged four, three, two and two years old respectively in 1982. Deducting the gestation period of 22 months and the age of the calf indicate an approximate sexual maturity at 22, 21, 18 and 15 years of age respectively for the females concerned. In addition, three females aged 20, 15 and 15 years old respectively presumably had not yet had their first calf. Although the possibility of neo-natal mortality cannot be ruled out, the ages of the latter females also serve as an indicator of fairly late sexual maturity. While the above data can only serve as an approximate indication of age at sexual maturity, it is postulated that in the northern Namib Desert, female elephant sexual maturity varies between 15 and 22 years of age. With the small sample size it is considered invalid to calculate mean age at sexual maturity.

The number of potentially mature females in the population at any one time will depend on the age at sexual maturity, e.g. the younger the age at sexual maturity, the more potential mature females in the population. Since calving interval is a function of the number of mature females during a specific year in the population in relation to the number of calves-of-the-year in that year (Croze 1972, Douglas-Hamilton 1972, Jachmann 1980), it follows then that the number of mature females in the population will influence the calculation of the calving interval. Thus, since the mean age at sexual maturity for the desert-dwelling population is unknown, it is only possible to relate the possible range in mean calving interval. Table 10 depicts different mean calving intervals over a period of time for varying numbers of mature females in the desert-dwelling population in accordance to different ages at sexual maturity. Data on calf mortality are lacking and the results shown in Table 10 should be regarded as the maximum calving interval since no allowance was made for mortality. It can therefore only serve as an approximate indication of mean calving rate. From Table 10 the possible mean calving interval over an eight-year period varied between 6,9 and 12,5 years in the desert-dwelling population.

Table 10: Possible range of the calving interval (years) in the desert-dwelling elephant population of the northern Namib Desert, South West Africa, between 1979 and 1986, calculated from different numbers of mature females in the population as would be determined by different ages of sexual maturity.

POPULATION PARAMETER	NUMBER OF MATURE FEMALES AND NEWBORN CALVES IN POPULATION DURING THE YEAR LISTED BELOW								MEAN CALVING INTERVAL*
	1979	1980	1981	1982	1983	1984	1985	1986	
Number of calves born	2	2	1	0	0	2	1	8	
Number of mature females:**									
Possible age at sexual maturity									
15 years	18	19	20	26	27	30	30	30	12,5
16 years	17	18	19	20	26	27	30	30	11,7
17 years	16	17	18	19	20	26	27	30	10,8
18 years	15	16	17	18	19	20	26	27	9,9
19 years	13	15	16	17	18	19	20	26	9,0
20 years	11	13	15	16	17	18	19	20	8,1
21 years	11	11	13	15	16	17	18	19	7,5
22 years	10	11	11	13	15	16	17	18	6,9

* Mean calving interval = Total number of mature females between 1979 and 1986, divided by the total number of calves born during that period.

** The number of mature females in the population during a specific year will depend on the possible age at sexual maturity e.g. the lower the age at sexual maturity the more potential mature females in the population.

COMPARISON BETWEEN THE DIFFERENT ELEPHANT POPULATIONS IN THE KAOKOVELD

Age structures

Figure 25 shows the simplified population structure of the eastern, transitional and western or desert-dwelling elephant populations in the Kaokoveld during 1982 in terms of percentage animals alive in each age class. As mentioned earlier, subadults and adults are presented as one class and no sex differentiation is made in the younger age classes. The frequency distribution of the simplified age classes of the three populations is not significantly different ($F = 0{,}754$; $p>0{,}05$; $df_1 = 2$, $df_2 = 9$), possibly as a result of the crude age class differentiation and the low numbers of elephants. However, some differences are apparent and might be biologically meaningful.

The percentage bulls older than 22 years in the eastern (9 per cent) and desert-dwelling (10 per cent) populations appeared to be similar but that of the transitional population (3 per cent) was alarmingly low. This low percentage of bulls in the transitional population can be directly related to a high incidence of hunting (legal and illegal) in 1980 and 1981 within the range of transitional elephant population (Fig. 18).

In the transitional population 43 per cent of the population consisted of animals less than 10 years old, followed by the eastern population with 27 per cent and the desert-dwelling

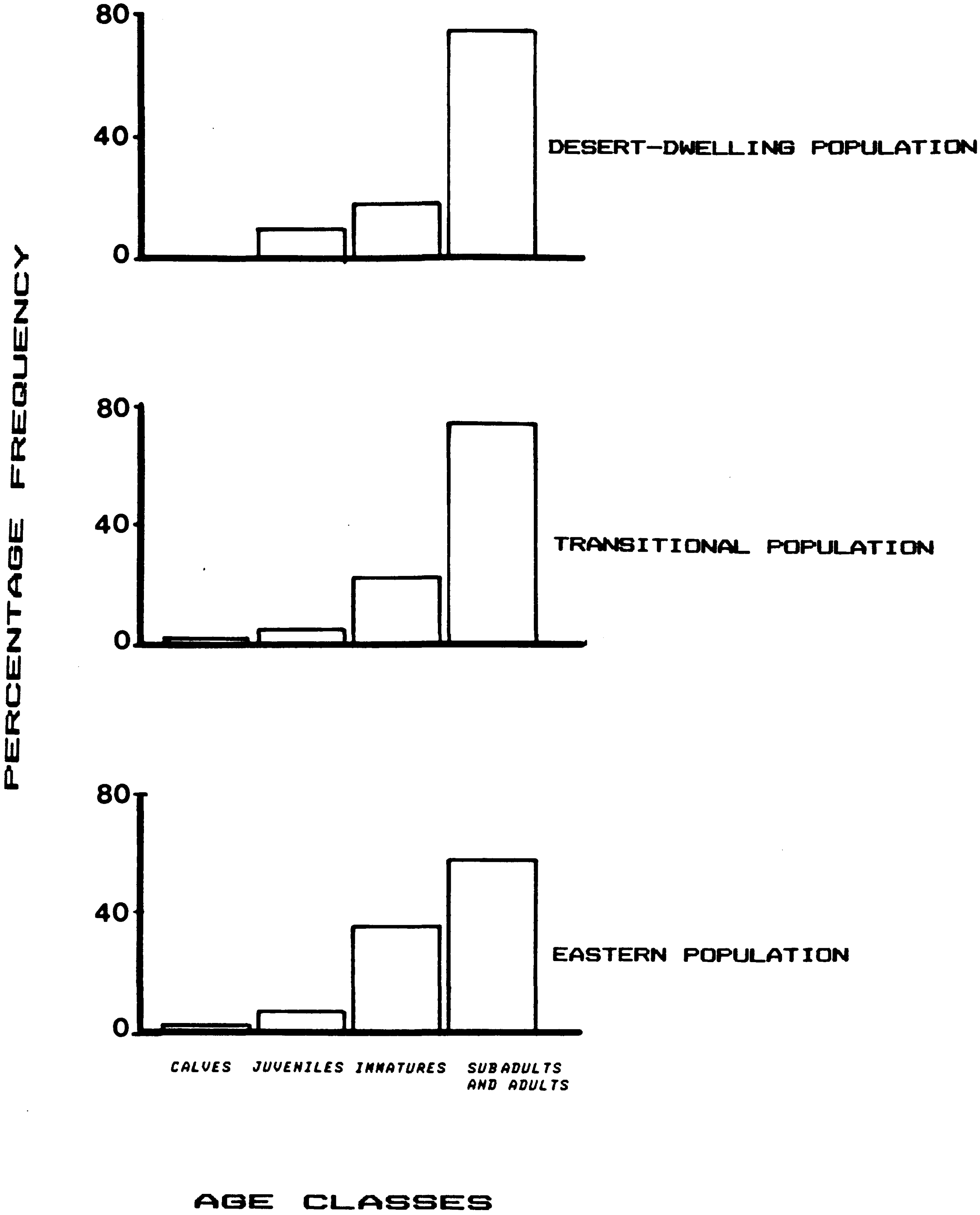


Figure 25: Comparison of the simplified age structures of the three elephant populations in the Kaokoveld, South West Africa, during 1982.

population with 26 per cent. Again the high percentage of immature animals in the transitional population could be the result of hunting selection for older (large tuskbearers) animals. The desert-dwelling elephant population had the highest percentage of animals (9 per cent) of less than three years old, followed by the transitional population with 8 per cent and the eastern population with 5 per cent. These latter juveniles in all three population must have been conceived (three years old plus two years gestation period) before the onset of the five year drought. The low number of calves less than one year old, in the Kaokoveld, can be ascribed to the devastating drought conditions (Chapter 2) as previously discussed.

Density

Table 11 illustrates the number of elephants per km^2 occurring in the Kaokoveld since 1970. Densities were calculated as crude densities in terms of overall elephant distribution. As can be expected from the rainfall and vegetation in the respective ranges, the eastern and transitional elephant populations occurred at higher crude densities than the western or desert-dwelling elephant population.

Unfortunately, no clear distinction was made between elephant populations prior to 1977 (Owen-Smith 1970, Joubert and Mostert 1975) and therefore trends must be compared in terms of all the elephants in the Kaokoveld. Assuming that the earlier population estimates were correct, the overall crude densities of all the

Table 11: Comparative crude densities (elephants/km^2) of the elephant populations in the Kaokoveld, South West Africa, between 1970 and 1983, derived from the observed distribution range of the elephants within the Kaokoveld.

POPULATION	1970*			1977**			1983		
	Number of elephants	Distribution range (km^2)	Density	Number of elephants	Distribution range (km^2)	Density	Number of elephants	Distribution range (km^2)	Density
Western	-	—	—	124	20290	,006	70	14750	,005
Eastern	-	—	—	376	15940	,023	207	7220	,029
Transitional	-	—	—				80	3500	,023
Total	800	53410	,015	500	36230	,014	357	25470	,014

* From Owen-Smith (1970) and Joubert and Mostert (1975). No distinction was made between populations.

** From Visagie (1977), Le Roux (1978) and Viljoen (1980). No distinction was made between the eastern and transitional populations.

elephants in the Kaokoveld remained virtually the same since 1970 (Table 11) despite a significant reduction of 52 per cent in the elephants' distribution range (χ^2=10351,6; p<0,001; df=2) and 55 per cent in elephant numbers (χ^2=185,09; p<0,001; df=2). The corresponding reduction in range and numbers while the overall crude density remained the same (χ^2=0,0001; p>0,05; df=2), support the observation that recent gaps in elephant distribution (Figs.7, 8 and 10) were caused by local extermination of elephants in certain areas and not by forcing elephants to emigrate to other areas in the Kaokoveld.

Regarding the western or desert-dwelling elephant population, there was a slight reduction in crude density since 1977 (Table 11) but a 42 per cent reduction in numbers. When only the areas enclosed by the 95 per cent home range polygons of the desert-dwelling elephants are considered, these elephants occurred at an ecological density of 0,007 per km^2 in 1983. Ecological density is considered more viable than crude densities which include their whole distribution range e.g. occasional wanderings outside their regular home ranges.

DISCUSSION

SOCIAL ORGANIZATION

Seasonal variation in elephant group sizes which are positively correlated to rainfall have also been observed in several other elephant populations in Africa (Buss and Savidge 1966, Laws 1969a, Watson and Bell 1969, Leuthold 1976a, Martin 1978, Barnes 1983). The tendency to aggregate can be explained as being primarily related to a temporary superabundance of food, and perhaps water. The dry-season break-up into smaller units, presumably reduces intra-group competition under conditions of food shortage (Douglas-Hamilton 1972, Barnes 1983, Western and Lindsay 1984). The breaking-up of groups, however, is limited to large feeding aggregations and does not extend beyond a certain minimum size. These minimum size groups remained constant even during periods of extreme food and water shortage, such as in 1981 in the northern Namib Desert. Thus, it appears that large group sizes are determined by the probability of feeding competition and therefore climatic conditions, and small groups (family units) by an inherent social order.

Specific individual female elephants of all ages, and males up to the age of 17 years, which are probably related to each other, group together in specific family units which show a remarkable cohesion and stability. Family units are always coordinated in their movements and each has a specific geographical range. Older mature bulls generally show no affinity with any family unit although younger bulls show a positive association with a specific family unit.

These observations confirm that the family unit is the basic stable unit in an elephant society which corresponds with that of other elephant populations in Africa (Buss 1961, Laws 1969a, 1970, Laws _et al_. 1975, Douglas-Hamilton 1972, Dublin 1983, Moss and Poole 1983). The work of Douglas-Hamilton (1972), Martin (1978), Moss and Poole (1983) and Hall-Martin (1987) also revealed evidence of organizational levels above that of the family unit consisting of bond groups or clans. It would appear that large feeding aggregations are limited to members of the same kin group or clan.

Male elephant social organization in the northern Namib Desert differ in pattern of association and social interaction from those of the family units. Adult bulls showed little affinity for other individual bulls or for individual family units. Individual contact generally seemed to be unstable and of short duration. The chance of ties might be related to the probability of intraspecific encounters rather than an underlying social order. There also appears to be no age order of association except in the case of the two younger bulls. However, intraspecific associations appeared to be positive as a relatively small proportion of the bulls' time was spent solitarily. During the wet season, bulls associated more with family units, forming part of feeding aggregations and during both the dry seasons there was a gradual increase in the number of solitary animals.

Again the social organization of elephant bulls in the northern Namib Desert corresponds with that of elephant bulls in other populations in Africa (Hendrichs and Hendrichs 1971, Douglas-Hamilton 1972, Croze 1974a, Laws _et al_. 1975, Barnes 1983, Moss and Poole 1983). However, there is no evidence in the present study to support the observation by Douglas-Hamilton (1972), later quoted by Laws _et al_. (1975), Dublin (1983) and Moss and Poole (1983), that young bulls are forcibly ejected from family units, shortly after reaching puberty. The progressively intermittent association of young bulls with a specific family unit over a prolonged period, suggests a gradual loosening of ties. This is also evident from the observations of Laws _et al_. (1975). Also, in the present study, there were no observations of any aggressive behaviour of females towards bulls of any age. In fact, females showed a remarkable tolerance towards other elephants. The forcible ejection of young bulls elsewhere, however, could be a function of elephant density as the population at Lake Manyara National Park has one of the highest densities of elephants in Africa (Douglas-Hamilton 1972) while those of the northern Namib Desert are the lowest known to date.

The social organization of the elephant lends itself to a dynamic survival strategy which is flexible and patterned in response to ecological conditions. Herd fusion and fission are not random but follow a predictable seasonal pattern of association between family units and bulls according to a hierarchal clustering into bond groups or clans and a break-down in a reverse order (Douglas-Hamilton 1972, Moss and Poole 1983, Western and Lindsay 1984). The formation of large groups possibly bears an advantage in terms of anti-predation (Laws _et al._ 1975, Dublin 1983) or holds reproductive benefits, such as improved mating opportunities (Western and Lindsay 1984). Seasonal breeding of elephants synchronized towards the rainy season is well documented elsewhere (Hanks 1969, 1972b, Sherry 1975, Smuts 1975, Guy 1976, Williamson 1976, Kerr 1978, Craig 1984). It follows then that most mating activities occur during the rainy season (Guy 1976) and hence among the large elephant congregations of several family units. Such congregations possibly improve the chances of reproduction as the chances of a female in securing a dominant male should also increase (Poole and Moss 1981) while at the same time the harassment of subordinate males is avoided (Western and Lindsay 1984). It would also minimize energy expenditure in search of mates. This could serve as a mechanism to ensure optimal fitness of the gene pool.

With the onset of the dry seasons, the preferred food supply becomes depleted and the large herds divide to maintain forage efficiency and to minimize interspecific competition for food. This breakdown of herds, however, only continues to a certain minimum level, the family unit, where closely related individuals have more to gain through inclusive fitness by maintaining group cohesion (Dublin 1983). Fragmentation of large herds also coincide with a general movement of each family unit to its exclusive dry season feeding grounds (Chapter 5). In this respect, resource location and the transmission of this knowledge about spatio-temporal resource distribution within the family unit might be of paramount importance. This is especially important in the northern Namib Desert with its limited and localized food and water resources. Knowledge about resource distribution might outweigh the disadvantages of interspecific food competition within the family unit.

AGE STRUCTURE

The variation in age class frequency in the age structure of the desert-dwelling elephant population is attributed to a variation in recruitment rate. The recruitment rate in turn is related to the effect of rainfall on the food plants of the elephants. The condition of the female might influence ovulation. During periods of optimal rainfall and its indirect effect on the nutritional status of food plants, the physical condition of females elephants might well induce oestrus and therefore higher conception rates (Laws et al. 1975). During years of low or no rainfall the nutritional status of the cows is severely depressed and the onset of oestrus might be delayed. Recruitment cycles linked to rainfall patterns have also been reported in other elephant studies (Laws 1969b, Croze 1972, Douglas-Hamilton 1972, Hanks 1972b, Laws et al. 1975, Sherry 1975, Kerr 1978, Jachmann 1980).

The above may explain the present variation in recruitment rate of the desert-dwelling elephants but it does not fit in with the general idea that calf survival is related to rainfall (Croze 1972, Corfield 1973, Leuthold 1976b, Jachmann 1980). A calf conceived two years hence might be born during a year of extreme drought, but the available data in the present study do not indicate a higher mortality during years of low rainfall. This lack of data might be attibuted to the possibility that neo-natal mortality might be high in years of low rainfall but that due to the small size and rapid deterioration of the carcasses, there is less chance of it being discovered in the field. It might also well be that births related to conception in high rainfall years were much higher than detected in this study and that the mortality of those calves born in years of low rainfall were also high but that enough calves survived to account for the peak in birth rate. Other factors might also be superimposed on the primary effect of rain in the year of conception. The nutritional effect of food plants on pregnant and lactating mothers in the years prior to low rainfall might also be of primary importance in affecting calf survival. Calves and mothers in good condition obviously have a greater chance to survive marginal climatic conditions.

Alternatively, variation in natality may be indirectly influenced by poaching and its subsequent disturbance as was pointed out by Laws et al. (1975), Jachmann (1980) and Lewis (1984). In the northern Namib Desert with its short rainy season, any disturbance during the rainy period might seriously affect mating activities and or the physiological condition of the females. However, poaching might also have a positive influence on the reproductive output via parameters such as the reduction of intra-specific competition for the available food, a possible explanation for the apparent lack of drought-induced mortality in the desert-dwelling elephants during the 1977-1981 drought when more than 80 per cent of the other animals died as a result of the drought (Viljoen 1982b). The high number of births during 1986 not only correspond to high rainfall during the year of conception, but also correspond to the period when there was an increase in law enforcement activities. This might indicate that disturbance due to poaching is an important factor but it might also only be a result of three successive years of high rainfall prior to conception.

Direct comparison of the age structures of the desert-dwelling elephants with those of other elephant populations in Africa is not possible since different methods were used (Croze 1972, Leuthold 1976b). Some age structures were derived from culling operations which depict only certain portions of the populations (Hanks 1972b, Laws _et al_. 1975, Smuts 1975, Sherry 1975, 1978, Kerr 1978) and different age class intervals were used. Generally, however, the age structure of the desert-dwelling population corresponds with that of other populations with a deficit in the younger age classes compared to a 'normal' age structure (Leuthold 1976b). The data of Douglas-Hamilton (1972) and Laws _et al_. (1975) generally show a higher frequency in the younger age classes, but this anomaly in the desert-dwelling population can probably be ascribed to the devastating drought conditions and poaching as described earlier.

SEX DETERMINATION OF ELEPHANT MANDIBLES

Laws _et al_. (1975) measured mandible length and found no significant differences between the sexes in the slope of the regression line although mandible length showed a close correlation with shoulder height for different elephant populations. It would therefore appear that mandible width, as measured in this study is more appropriate to distinguish between the sexes at a given age. However, the results must be approached with caution since the present sample size is small and it might only be applicable to the conditions existing in the Kaokoveld.

With the above reservation in mind, sexing of older elephant carcasses ($\geq$15 years) in the Kaokoveld appears valid as the mandibles examined clearly fall into one of the two width classes at a given age. It applied equally successfully to carcasses belonging to the transitional elephant population. It was thus subsequently used to determine the sex ratio of the desert-dwelling elephant population.

Although a high correlation between mandible width and age for each sex separately has been demonstrated, differences in mandible width between successive ages in a given sex class are small (1,6 to 5 mm) and it is doubtful if such a small difference can be accurately measured in the field. Nevertheless, the width of a mandible from an elephant of known sex can serve as a rough guide to assigning a given age class.

SEX RATIO AND AGE

The sex ratio of elephants in the desert-dwelling population correspond with that of most other elephant populations in Africa in terms of a parity in younger or immature elephants (Croze 1972, Hanks 1972b, Corfield 1973, Sherry 1975, Smuts 1975, Kerr 1978, Jachmann 1980 and 1986) and a departure from unity in the older animals (Laws 1969b, Corfield 1973, Laws et al. 1975, Jachmann 1980 and 1986, Lewis 1984). This indicates a sex-specific mortality in favour of females in the older age classes. This can possibly be explained by hunting selection as hunters tend to select animals for their tusks which would necessary mean that more bulls will be killed.

In the absence of selective hunting, the natural sex ratio of older animals (≥15 years) would possibly also be inclined towards parity as Smuts (1975) found an equal sex ratio in older animals in the Kruger National Park, an area where poaching and thus selection of mature bulls is suppressed. Sex-specific mortality (poaching?) in the northern Namib Desert must have started before 1979 as inclusion of shot elephant carcasses still resulted in a sex ratio skewed towards female abundance in adult elephants.

AGE AT SEXUAL MATURITY AND MEAN CALVING INTERVAL

Regardless of possible calf mortality, it is clear that the mean calving interval varied considerably form year to year, emphasizing the dangers of extrapolating calving interval from any one year. Taking a midpoint of 19 years of age from the possible range in age at sexual maturity for females in the desert-dwelling elephant population, the population was in a declining phase up to 1983 with a mean calving interval of 13,2 years. Between 1984 and 1986 however, the population appeared to be increasing with the mean calving interval reduced to 6,6 years. Using any one of the latter phases for extrapolation would probably lead to a gross misinterpretation of future predictions.

Table 12 summarizes data on the calving interval and the age at sexual maturity from the present study and from that of other elephant populations in Africa. Although not strictly comparable since the data from other populations have mainly been derived from post-mortem studies in samples collected within the space of a few months, the age at sexual maturity and calving intervals of desert-dwelling elephant population falls within the range of that of other populations. However, both sexual maturity and calving interval in the desert-dwelling population appear to be high in relation to most other populations, indicating some sort

Table 12: Data on the calving interval (years) and the age (years) at sexual maturity for different elephant populations in Africa. From Laws et al. (1975), Sherry (1975), Smuts (1975), Williamson (1976), Kerr (1978), Jachmann (1980) and the current study.

LOCATION	CALVING INTERVAL	AGE AT SEXUAL MATURITY
Mkomazi	2,6 - 3,4	12,24
Mkomazi East	3,1 - 5,0	12,18
Tsavo National Park	5,1 - 10,3	11,73
Murchison Falls National Park, North	7,5 - 11,5	12 - 15
Murchison Falls National Park, South	4,8 - 6,8	11 - 22
Budongo Forest Reserve	5,4 - 13,5	22,38
Luangwa Valley National Park	3,5 - 4,0	14,00
Kasungu National Park	2,2 - 5,3	11,00
Kruger National Park	4,0 - 5,0	7 - 15
Lake Manyara National Park	2,9 - 12,0	6 - 16
Gonarezhou National Park	3,6 - 4,9	12 - 13
Mana Pools National Park	3,5	12 - 13
Northern Namib Desert	6,9 - 12,5	15 - 22
Wankie National Park	3,9 - 4,7	9 - 15

of depressing factor.

Buss and Savidge (1966), Laws (1969b) and Laws _et al_. (1975) have presented evidence indicating that density-related population regulatory mechanisms result in variations in fertility and mortality rate in elephants. In the northern Namib Desert the crude elephant density is 0,005 elephants/km^2 and large areas of potentially suitable habitat is unoccupied following the reduction in elephant numbers from 124 in 1977 to 70 in 1983. Therefore, the presumed high sexual maturity and calving intervals in the desert-dwelling population could not have been the result of density-dependent stresses.

In the northern Namib Desert with its highly erratic and low rainfall it can be expected that the environment would be the major factor influencing fertility. It has already been shown that conception is closely related to rainfall and hence the nutritional status of the elephants is probably the important factor in determining reproduction parameters. It follows then that females potentially ready to ovulate at 15 years of age would be inhibited if their nutritional status is low, such as in a dry year. Thus, a female reaching the age of 15 years in 1977, a year of low rainfall (Table 3) would probably not have ovulated or alternatively she would not have conceived since food production and hence her nutritional status would have been low. Similarly, the same female would probably not have conceived in the following years. Only in 1982 when the female was 20 years old, would her nutritional status have improved to such an extent due to a higher rainfall and the resultant food production, that she would have conceived. This was indicated in the present study when a female aged 20, and which presumably had not yet conceived, was observed mating in 1982. Thus, she would have produced her first calf in 1984 at the age of 22 years. It is here concluded that in the desert-dwelling elephant population, although the females might potentially reach sexual maturity at the same age as in other elephant populations, the functional age at sexual maturity is not constant but will vary in accordance with climatic conditions. The same argument can be applied to the mean calving interval which seems to vary from year to year in close correlation with the environmental conditions during the year of conception.

Another factor which might have contributed to a reduction in fertility in the desert-dwelling elephant population could have been the combined effect of poaching and hunting activities, with the resultant disturbances as discussed previously. In Bunyora, Uganda where an elephant cull was undertaken between 1946 and 1966, Laws _et al._ (1975) found that instead of hypothetical compensating mechanisms coming into play to increase population growth, there appeared to be a decrease in birth-rate, an increased natural mortality, a slower growth rate and a later sexual maturity. On the other end of the scale, the elephant population of the Addo Elephant National Park, South Africa, increased from 18 to 102 elephants in 26 years following the erection of an elephant-proof fence (Hall-Martin 1980). With environmental factors remaining the same this can only be contributed to a decrease in illegal hunting and disturbance. Prior to the erection of the fence the Addo population was stable or decreasing due to illegal hunting. Thus, in the northern Namib Desert, the low calving interval recorded between 1979 and 1982 was probably the result of both environmental conditions and disturbances. The increase in births following 1982 not only correspond with a higher rainfall but also with an increase in law enforcement activities.

It is thus concluded here that in the northern Namib Desert, both sexual maturity and the mean calving interval will vary according to climatic conditions and that hunting also have a negative influence on the fertility rate.

COMPARISON BETWEEN POPULATIONS

Age structure

The simplified age structure of the elephant populations of the Kaokoveld, which incorporate the ages of shot elephants, is presented in Figure 26 together with that of the Etosha National Park elephants (De Villiers 1981).

Although the data are inadequate to reach any significant conclusions there appears to be no marked superficial differences

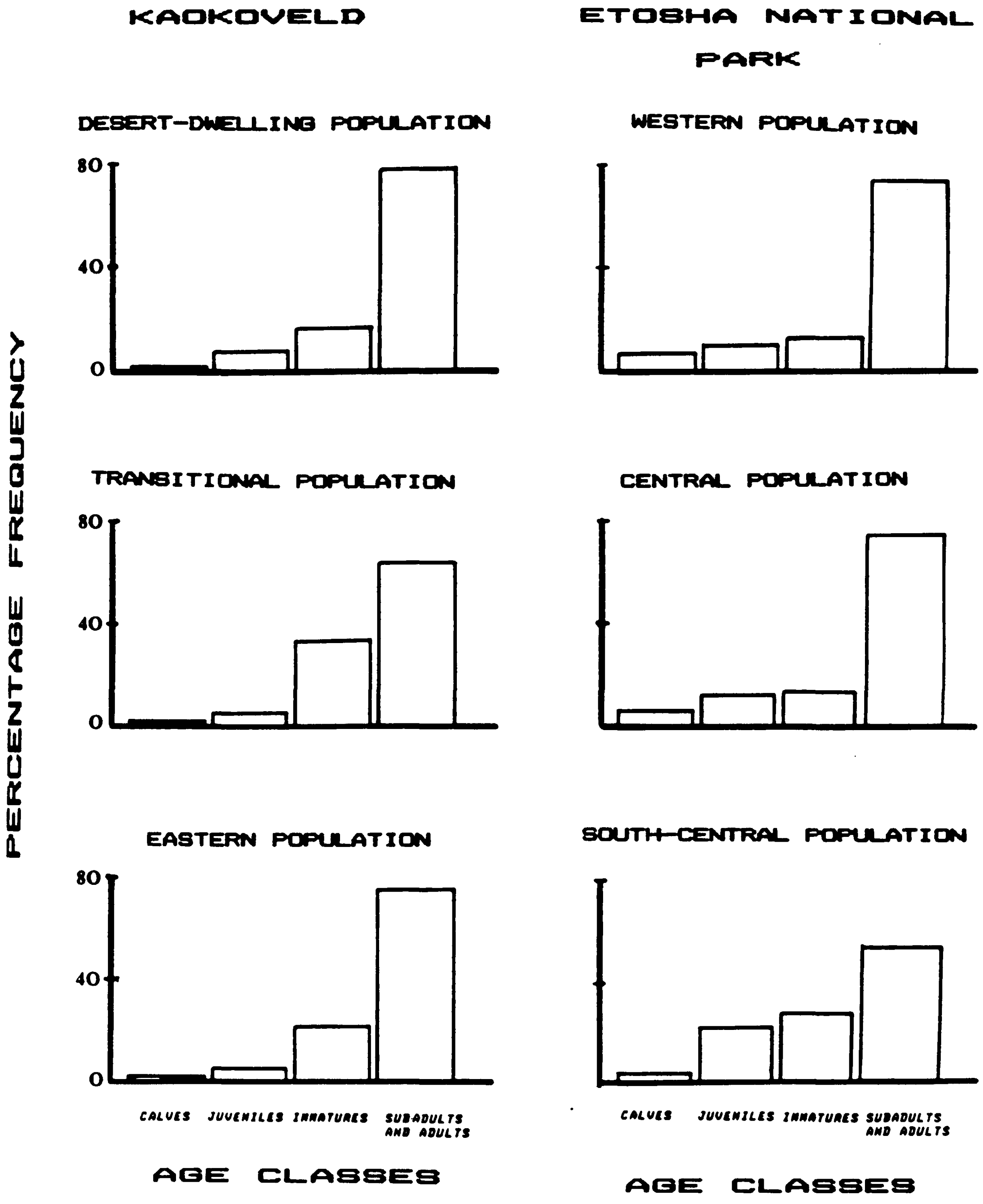


Figure 26: Comparison of the simplified age structures of the elephant populations in the Kaokoveld (incorporating ages derived from shot elephants) and those of the Etosha National Park (De Villiers 1981), South West Africa.

in the age structures of elephants from the Etosha National Park in the east to the northern Namib Desert in the west. The relatively higher frequencies of calves and juveniles in the Etosha National Park can probably be attributed to the higher rainfall before 1977-1978 when the latter age structures were constructed (De Villiers 1981). This corresponds with the higher frequency of immatures (which were been born in 1977-1978) in the 1982 age structures of the Kaokoveld populations. This again illustrates the effect of the higher rainfall prior to the drought conditions between 1977 and 1982.

Thus, the age structure of the desert-dwelling elephants appear to be on par with that of other elephant populations occurring in higher rainfall areas with presumably more suitable habitat. The desert-dwelling elephant population appear to be demographically viable with a relatively large percentage of young animals and with a large percentage of potential breeders. There is therefore no evidence to suggest that the relatively harsh environmental conditions had had a negative effect on the desert-dwelling elephant population in comparison with other populations of elephants occurring elsewhere in more suitable habitat.

Elephant density

Comparison between past and present elephant densities (Table 11) in the Kaokoveld supports the observations on home range fidelity made in this study (Chapter 4). The observed gaps in elephant distribution (Figs. 7,8 and 10) and corresponding reduction in numbers were thus clearly caused by local extermination of elephants and not by emigration to other areas in the Kaokoveld.

Elephant densities in the Kaokoveld are considerably lower than that recorded in other African areas (Table 13), and this probably reflects the influence of rainfall and primary production, which is considerably lower than those of the other areas studied. Although elephant density seems to increase with an increase in rainfall no significant linear correlation (r=0,045; t=0,218; p>0,05; df=24) between rainfall and elephant densities could be found from the data in Table 13. This is probably because of differences in the methods used and also other factors which might have influenced the primary production of a given area (Coe, Cumming and Phillipson 1976, Short 1983). However, when comparing only those regions with a rainfall of less than 600 mm per annum and for which the elephants are reported to be on par with the carrying capacity of the respective regions (Glover 1963, Van Wyk and Fairall 1969, Penzhorn, Robbertse and Olivier 1974, De Villiers 1981), a significant linear correlation could be found (r=0,694; t=2,367; p<0,05; df=7). It might therefore be valid to make predictions in terms of elephant biomass and carrying capacity from the available meteorological data (Chapter 7).

POPULATION DYNAMICS

One of the main difficulties encountered in determining possible population trends in this study, was the lack of suitable data on

Table 13: Comparative densities (elephants/km^2) of elephants from various regions of Africa with differing rainfall (mm) regimes.

REGION	DENSITY	RAINFALL	SOURCE
Kaokoveld, South West Africa			
Western population	0,005	30 - 100	This study
Transitional population	0,023	100 - 150	This study
Eastern population	0,029	150 - 350	This study
Etosha National Park, South West Africa	0,14 - 0,43	250 - 450	De Villiers (1981).
Amboseli, Kenya	0,14	350	Western & Lindsay (1984).
Addo Elephant National Park, South Africa	2,70	442	Penzhorn, Robbertse & Olivier (1974).
Mkomazi, Kenya	0,82	480	Watson, Parker & Allan (1969).
Kruger National Park, South Africa	0,40	580	Van Wyk & Fairall (1969).
Tsavo National Park, Kenya	1,25	553	Laws (1969a).
Sengwe, Zimbabwe	1,00	600	Anderson & Walker (1974).
Zambesi Valley, Zimbabwe	0,34	650	Kerr & Fraser (1975).
Kidepo Valley National Park, Uganda	0,35	715	Ross, Field & Harrington (1976).
South Western Niger	0,024	750	Poche (1974).
Serengeti National Park, Tanzania	0,104 - 0,263	803	Watson & Bell (1969).
Lake Manyara National Park, Tanzania	5,00	915	Douglas-Hamilton (1972).
Murchinson Falls Park, Uganda	1,9 - 3,8	1145	Laws (1970).
North Bunyoro, Uganda	0,40	1150	Eltringham & Malpas (1980).
Rwenzori National Park, Uganda	1,43	1200	Eltringham (1977).
Bia National Park, Ghana	0,33	1500	Short (1983).
Gola North, Sierra Leone	0,10	2800	Merz (1986).
Gola East, Sierra Leone	0,27	3200	Merz (1986).

natural mortality. Assuming that the 1977 population estimates were correct, there was a reduction of 31 per cent in the desert-dwelling elephant population between 1977 and 1980. At the same time, according to the combined age structure (Figure 22), a minimum of five elephants were added to the population. Thus at least 43 elephants (38+5) or 33 per cent of the population died between 1977 and 1980. This amounts to a mortality rate of 11 per cent per annum. Following the same procedure, the annual mortality between 1980 and 1982 was 9 per cent. Between 1982 and 1986 there is no recorded mortality in adult elephants (Owen-Smith 1986, S.Brain pers. comm. 1986) and no data on calf mortality. The above percentages must thus be regarded as minimum rates since possible neo-natal or calf mortality could not be taken into account.

However, since it has been shown that at least 71 per cent of the above mortality was caused by poaching, it is not representative of the natural mortality. Neither can elephants which died from unknown causes represent natural mortality as they probably also included wounded elephants which died later. Poaching or hunting and natural mortality are also not independent of each other. If poaching stops, natural mortality would increase because in the absence of poaching many animals that would otherwise have been shot are now at risk of death from other agents.

S.Brain, Skeleton Coast Park, P/bag 5001, Swakopmund, S.W.A.

The problem is that while poaching is a real and important cause of mortality in elephant populations it is not regular nor predictable. It can vary from as low as 1 per cent, such as in 1982 to as high as 21 per cent of the population such as in 1980 in the Kaokoveld. Thus, while populations dynamics can be worked out to the finest detail, the whole population structure can be altered, or even the whole population can be exterminated in one poaching spree.

Neither can the frequency variation in successive age classes in the desert-dwelling elephant population be used to calculate possible survival or mortality rates such as in life-tables since it has been shown that variation in age class frequencies is related to variations in recruitment rate and not to mortality. Also life-tables can only be valid when derived from a stable age distribution where the frequency of age class X is equal or greater than that of age class X + 1 (Croze 1972, Corfield 1973, Hanks and McIntosh 1973, Caughley 1977), which was not the case in the present study.

There is also evidence from the data in this study that both age at sexual maturity and calving interval can vary according to climatic conditions. Thus, any prediction or population simulation models based on parameters derived from any one period, might lead to highly erroneous results.

The only parameter judged here to give a reasonably reliable account of population trends in this study, is the general measure of observed exponential rate ($\bar{r}$) of increase or decrease (Odum 1971, Caughley 1977). The observed exponential rate of increase or decrease summarizes changes in population sizes over a number of years, and carries no assumptions about constant rate of increase, constant supply of food or stable age distribution (Caughley 1977) and is derived from the general formula:

$$N_t = N_o e^{rt}$$

where N_o represents the population size at time zero, N_t the size at time t and e the base of natural logarithms.

The observed rate of decrease and increase between 1977 and 1986 in the desert-dwelling elephant population are summarized in Figure 27 which depict changes in population sizes together with possible expected trends. From Figure 27 it can be seen that the population declined between 1977 and 1982 with an observed yearly rate of decrease of -0,11. If this trend continued the population would have halved in six years time. However, from 1983 the population increased at a rate of +0,048 or 4,8 per cent per year and if this trend continues the population will double by 1997.

The turning point was 1982 which corresponded with an increase in rainfall and in law enforcement and the subsequent decrease in mortality caused by poaching. Referring back to Figure 23, again with the reservation that possible calf mortality is not taken into account, the minimum number of calves (<one year old)

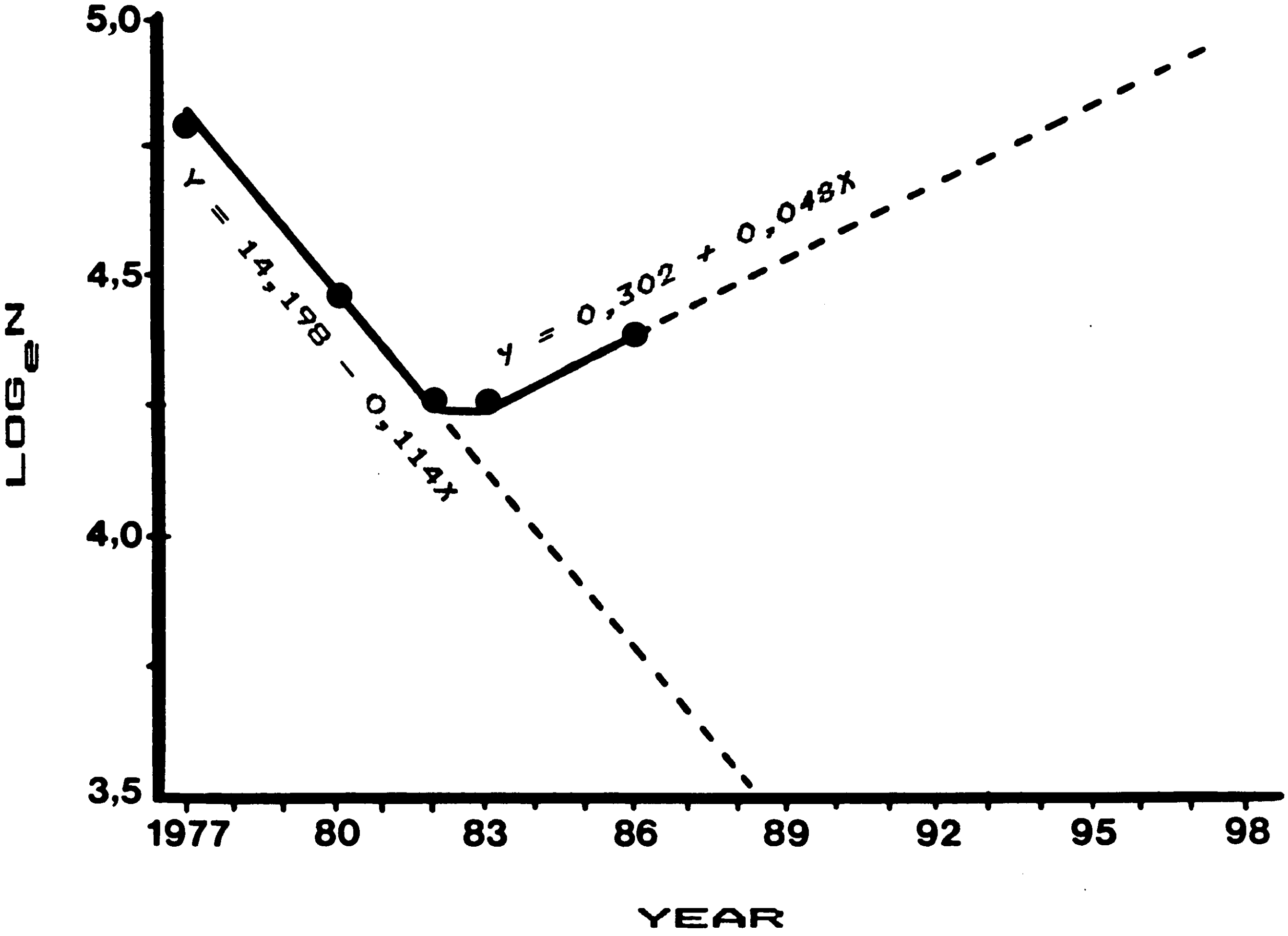


Figure 27: Plots of the natural logarithms of observed population size against time for the desert-dwelling elephants between 1977 and 1986 in the northern Namib Desert, South West Africa. Broken lines indicate possible population trends between 1987 and 1998.

observed between 1977 and 1981 was 11 or 2,2 per year. By the same calculation the number of calves observed between 1982 and 1986 also amounted to 2,2 per year. Thus it would appear that mortality and not a reduction in fecundity was the cause of the population decline up to 1982.

Hanks and McIntosh (1973) considered an annual population increase of four per cent to be close to the maximum rate (r_m) of increase for elephant populations. However, in the Addo Elephant National Park the population increased at a rate of 7 per cent which could be attributed to a low neo-natal and juvenile mortality in the protective sanctuary of the Park (Hall-Martin 1980). Thus, if mortality caused by poaching and disturbance in the northern Namib Desert can be eliminated, it is postulated that the desert-dwelling elephant population would initially increase at a relatively high rate despite possible adverse climatic conditions.

CONCLUSION

Mortality caused by poaching was the main population limiting factor and the recent cause of the decline in the desert-dwelling elephant population. Environmental conditions influence recruitment rate and are probably the main cause of a possible increase in age at sexual maturity and mean calving interval. However, although both age at sexual maturity and mean calving interval appear to be high it is still within the range of that of other elephant populations in Africa (Table 12). The age structure, sex ratio, social structure and social organization of the desert-dwelling elephants all correspond with those of other elephant populations in presumably more suitable habitats. Observations between 1983 and 1986 confirm that the internal population structure is still viable in the absence of human-induced predation and that the presumably unsuitable environment probably played a minor role in the population decline up to 1982.

The social organization of the African elephant, as manifested in the desert-dwelling elephant population, is regarded as one of the most advanced of all mammalian social systems (Dublin 1983). Group cooperation with the concurrent interdependence and mutual support provide advantages of inclusive fitness, allomothering, reduced juvenile mortality and transmission about resource distribution, making the African elephant well adapted to the adversities of an arid environment.

CHAPTER 5

SPATIAL DISTRIBUTION AND MOVEMENTS OF THE DESERT-DWELLING ELEPHANTS IN THE NORTHERN NAMIB DESERT.

INTRODUCTION

The presence of elephants in the northern Namib Desert region of the Kaokoveld, South West Africa, has led to many arguments and theories regarding their origin and movements. Bigalke (1958), Tinley (1971) and Woods (1973) believed that these elephants migrated from the Etosha National Park. The validity of these statements, however, has been questioned by Owen-Smith (1970), Viljoen (1980) and De Villiers (1981) on the basis of their studies in the Kaokoveld and the Etosha National Park.

Against this background, the present study was initiated to investigate relevant aspects of the movements and spatial organization of the desert-dwelling elephants. The immediate objective was to determine home range sizes, movement patterns and seasonal distribution of individual elephants. The ultimate aim was to relate these to environmental conditions and to obtain a clearer picture of long-term habitat utilization and the factors influencing it. Three hypotheses were tested: firstly, that these elephants migrate seasonally to and from the Etosha National Park; secondly, that these elephants are restricted to the desert region of the Kaokoveld; and thirdly that these elephants represent a discrete population with limited contact with the eastern populations.

As mentioned previously, the Kaokoveld comprises 11 million ha which is inhabited by some 30 000 people, the majority being situated at the main administrative centres in the east. Vast tracts of land are thus uninhabited by people and the area west of the 150 mm isohyet is practically devoid of people and fences, offering unrestricted movement to the elephants. Even in the east, the presence of people is no major limiting factor of elephant movements as is illustrated by the current distribution of the eastern elephant population (Chapter 3). Current restrictions to the movements of the desert-dwelling population of elephants are a veterinary fence in the south-east and the Atlantic Ocean in the west. There are no other fences in the region and movement to the north is unrestricted into southern Angola. To the east there are uninhabited (people) corridors to the Etosha National Park and Owamboland. Therefore, relative to most other areas in Africa, the information on elephant movements gathered in the present study is regarded as representative of the natural movements of an elephant population occurring at a low density in an arid environment.

For the purpose of the present study migration is defined as a seasonal two-way movement, involving a return to the area originally vacated and which usually follows traditional pathways

(Smith 1966). Occasional wanderings are defined as infrequent movements outside an elephant's home range which do not follow a seasonal pattern. Daily movements are defined as those movements the elephants undertake in their normal daily travels between food and water sources. Long-distance movements are defined as those movements which exceed the normal daily range. It usually occurs during seasonal migrations but may also include occasional wanderings. Home range is simply defined as the area over which an animal habitually travels while engaged in it's usual activities (Smith 1966). It follows then that a home range also reflects the distribution of an individual animal or group. Core areas are defined as those portions of the elephant's home range that exceed on equal-use pattern (Samuel, Pierce and Garton 1985). The definition of the term 'family group' follows those given by Buss (1961) and Douglas-Hamilton (1972), as previously described.

METHODS

Data were collected at two levels:

1. Recording the overall distribution and movement patterns of the population during aerial and ground surveys.
2. Determining the movements and home ranges of individual elephants, by reference to visually identifiable animals during ground surveys.

DISTRIBUTION PATTERNS

Monthly and seasonal distribution patterns and movements were determined during monthly aerial surveys, supplemented by ground surveys as previously described (Chapter 4). To minimize bias in the analysis of seasonal distribution and movements as well as space use patterns, only the first observation of an individual elephant or group in any one month was used in the analysis.

INDIVIDUAL IDENTIFICATION

Individual elephants were recognised by natural characteristics as previously described (Chapter 4). The movements of the identified elephants were then determined during extensive ground surveys between October 1980 and January 1982.

HOME RANGES

Home ranges were delineated by the minimum convex polygon method, using 95 per cent of the closest locations of an individual elephant or family group (Mohr 1947, Stickel 1954, Messier 1985). For this, the most peripheral locations of an animal were connected by straight lines and the area thus enclosed was measured by a compensating planimeter. In some cases the method of home range determination deviated slightly from the straight line polygon in that allowance was made for the veterinary fence in the south-east of the study area and the dune fields in the north-west. Here the boundaries of the adjacent home ranges follow the boundaries of the fence or the contours of the sand dunes. This was due to the fact that the elephants concerned were never actually recorded east of the veterinary line or in the dune area between Möwebaai and the Hoarusib River. Home ranges were assumed to be defined when the observation-area curves attained an asymptote (Odum and Kuenzler 1955, Bowen 1982, Messier 1985). Home ranges for bulls were calculated individually. As cows appeared to be permanently associated with other known cows, the home ranges of females and their offspring, were calculated in terms of their respective family groups (units) rather than as individuals.

The above method, however, gives no indication of the intensity and temporal pattern of utilization in a home range and the areas thus determined may be considerably larger than those normally utilized by the animals concerned. To determine the space-use pattern of a given elephant within its home range, the observed locations were plotted on a 1:250 000 map overlayed by a grid of 25 km^2 units. The frequency distribution of the number of 25 km^2 units containing 0,1,2,3.....n observed locations was then tested for randomness by comparison with the Poisson distribution. Areas of high occupation were visually identified and the percentage occupation was compared to other areas in the home range. Those areas which contained at least 25 per cent of all observed locations were defined as core areas (Samuel Pierce and Garton 1985). For this type of space-use patterns, a visual representation was considered to be the simplest way to convey the information.

DAILY MOVEMENTS

The daily movements of the desert-dwelling elephants were recorded by plotting the course travelled by a given elephant during 12-hour periods on a 1:250 000 map. The actual meandering courses during the normal daily activities of the elephants were measured, rather than measuring the straight line distance between consecutive locations, as the latter is only an indication of a daily shift in position and gives no indication of the actual distances travelled (Douglas-Hamilton 1971, Leuthold 1977). Data were collected separately for the sexes and between day and night on a monthly basis.

The quantification of diurnal movements of the elephants are based on information collected while following them on foot. The wary nature of the elephants precluded the use of ground vehicles. Any foreign smell or sound caused the elephants to react violently, making subsequent observations meaningless. The usual procedure was to locate the elephants by vehicle and from there to follow them on foot. By staying downwind and by not making any unnecessary sounds the observer could get to within 20 m of the elephants without detection as their eyesight seemed to be restricted during the day. During the night or on overcast days the elephant's eyesight seemed to improve and they could not be approached closer than 40 m. Camouflaged clothing seemed to be unnecessary as long as no sudden movements were made by the observer. For the quantification of nocturnal movements an elephant's spoor was followed by day on a scrambler motorbike from where the elephants were last seen on the previous evening. The course followed by the elephant was then plotted on a map.

Ideally, data for diurnal and nocturnal movements were collected consecutively within the same month, but it often happened that wind obliterated the spoor during the night in the loose sand of the river courses. In these cases only the diurnal distance moved was recorded. At times it also happened, that after following the tracks of the previous evening, the elephants themselves were only encountered late the following day, in which case the distance moved was recorded on a 24-hour basis. Mean values are followed by one standard deviation (±) of the mean.

LONG-DISTANCE MOVEMENTS

Long-distance movements were recorded in order to investigate possible migration patterns and routes. For the examination of long-distance movements, only linear distances between successive monthly locations which were 30 km or more in extent, well in excess of the elephants' mean normal daily movements of 25,74 km were taken into account.

WATER-RELATED MOVEMENTS

Water-related movements were recorded as the distance an individual elephant or group were observed from a water point. Only observations from the Hoanib River in the 1981 drought during the hot dry season, a period when there was no doubt as to the location of permanent water-holes, were used in the analysis. In 1982 widespread rains created a number of temporary water-holes, some of which lasted into the dry season and it was at times impossible to analyse their degree of utilization by the elephants. Likewise, observations in areas such as the Hoarusib River and Wêreldsend, both areas with an abundance of natural springs, could not be used in the calculations. Observations of elephants at water points or where the elephants were obviously in the process of moving between water points and feeding grounds, were excluded from the analysis.

RESULTS

HOME RANGES

For the determination of home range size, all locations of an individual elephant were mapped and measured in a chronological sequence and plotted against a time axis. The resultant observation-area curves (Figs. 28 and 29) illustrate the relationship of home range size to the period of observation. The data indicated that these relationships vary considerably between individuals. Using attainment of an asymptotic value as a

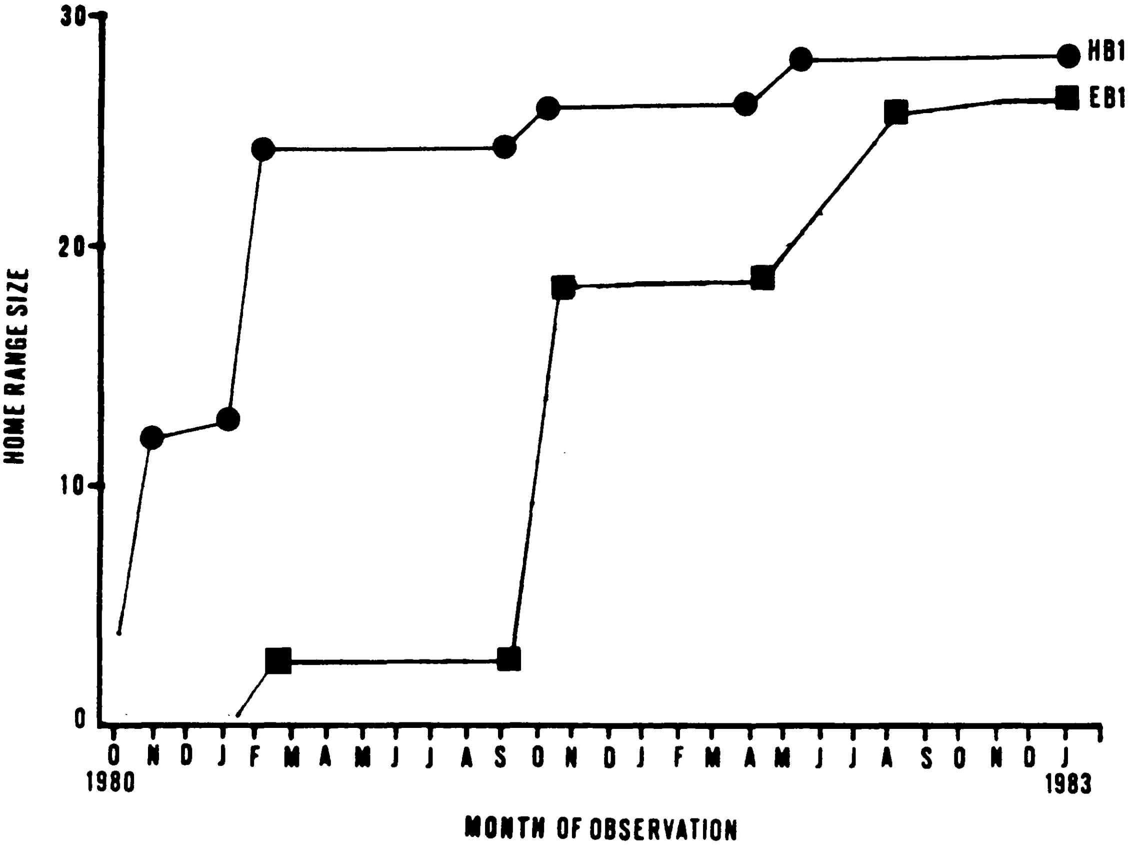


Figure 28: Cumulative observation-area curves, illustrating the relationship between home range size (100 km^2 units) and period of observation for two desert-dwelling elephant bulls in the northern Namib Desert region of the Kaokoveld, South West Africa.

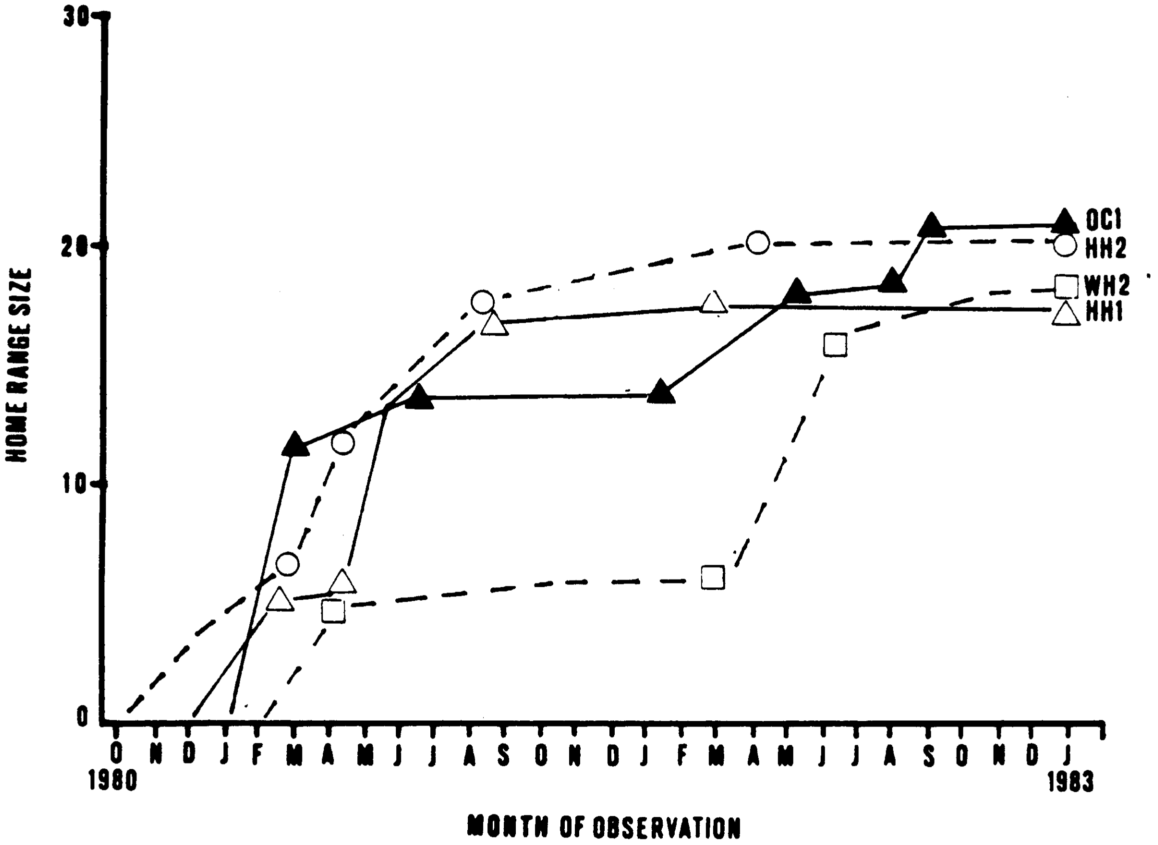


Figure 29: Cumulative observation-area curves, illustrating the relationship between home range size (100 km^2 units) and period of observation for four desert-dwelling elephant family groups in the northern Namib Desert region of the Kaokoveld, South West Africa.

criterion, five months of tracking appeared to be sufficient in one case (e.g. HB1, Fig. 28), while others (e.g. OC1, HH2 and WH2) required at least 18 months of observation (Fig. 29). By calculating the percentage area of all the actual home ranges defined by observation periods of five-month intervals, five months of observation reflected on only 33,9 per cent of the actual home range areas, ten months on only 65,5 per cent, 15 months on 69,8 per cent and 20 months on 82,1 per cent. At least 24 months of observations were required to estimate mean asymptotic home range size.

Thus, sufficient information was obtained to calculate eleven home range sizes representing 52 of the desert-dwelling elephants. No asymptotic values were obtained for the elephants that frequented the Kunene River area, for one family group in the Rooiplaat-Wêreldsend area, for two young bulls and for three of the seven surviving adult bulls.

The eleven home ranges ranged from 1 763 to 2 944 km^2, with a mean and standard deviation of 2 172,3 ± 436,5 km^2 (Table 14). For bulls (n = 4) the mean home range size was 2 698,4 ± 163,8 km^2 and for family groups (n= 7) 1 871,6 ± 119,1 km^2. The difference between the home range size of bulls and family groups was significant (t = 8,7068; p<0,001; df= 9).

Figures 30 and 31 show the location and shape of the home ranges of two bulls and four family groups. The home ranges of two bulls (NB1 and LB1) were virtually identical to that of EB1 and are

Table 14: Summary of data on six adequately defined home ranges (km^2) for the desert-dwelling elephants of the northern Namib Desert, South West Africa, during the period 1980 to 1983.

INDIVIDUAL OR GROUP REFERENCE NUMBER	HOME RANGE SIZE	MONTHS OF OBSERVATION	NUMBER OF RECORDS	GREATEST LINEAR DIAMETER (KILOMETRES)	MAXIMUM DISTANCE MOVED BETWEEN SUCCESSIVE LOCATIONS (KILOMETRES)	SEX
HB1	2944,0	28	78	115,0	97,8	BULL
EB1	2616,5	27	56	127,5	77,5	BULL
OC1	1907,5	29	63	98,3	90,0	FAMILY GROUP
HH1	1763,0	25	59	77,5	70,0	FAMILY GROUP
HH2	2031,0	25	56	90,0	74,5	FAMILY GROUP
WH2	1803,0	29	32	68,3	61,0	FAMILY GROUP

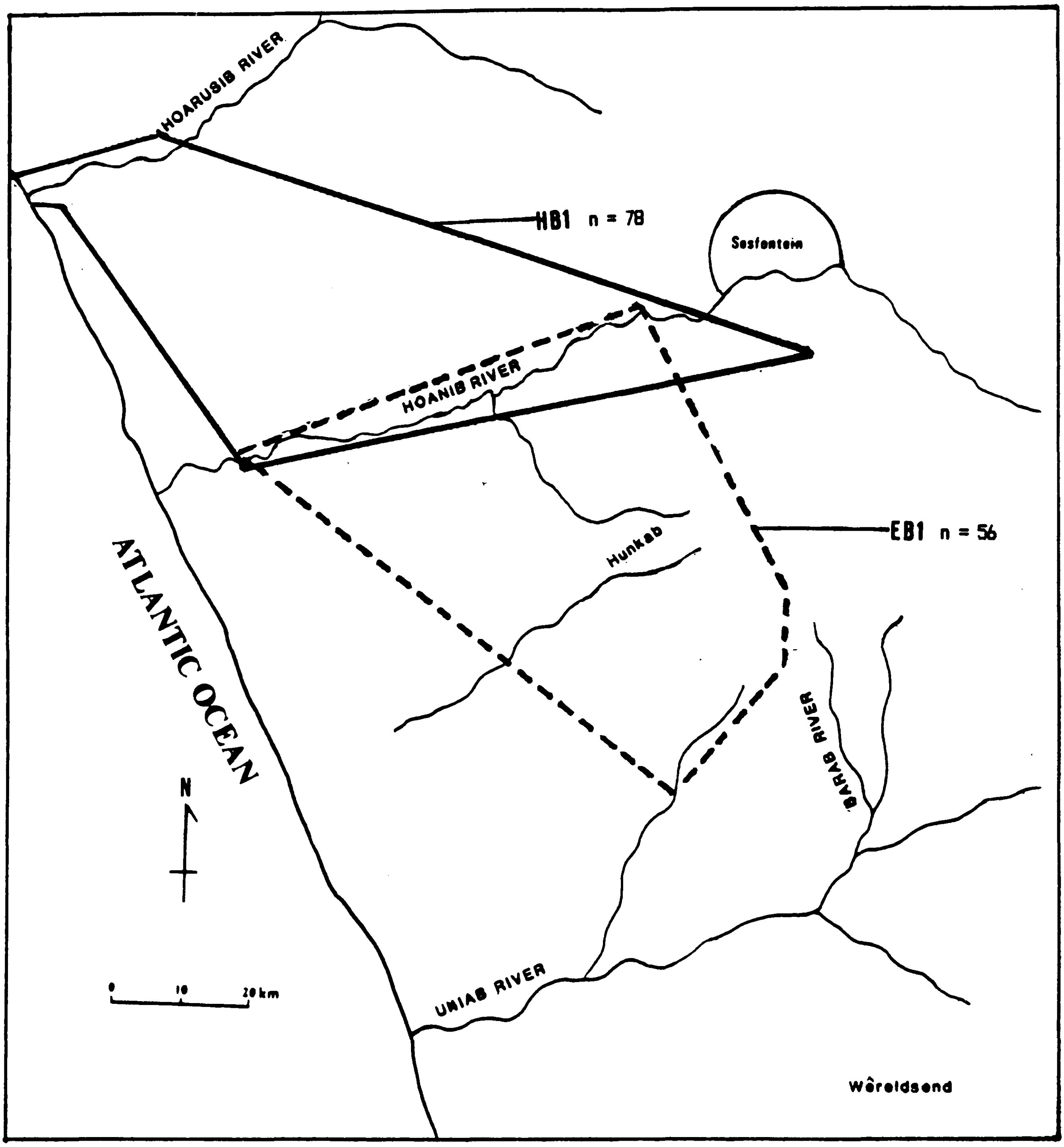


Figure 30: Spatial distribution of adequately defined home ranges for two bull elephants (HB1 and EB1) in the northern Namib Desert region of the Kaokoveld, South West Africa, between 1980 and 1983.

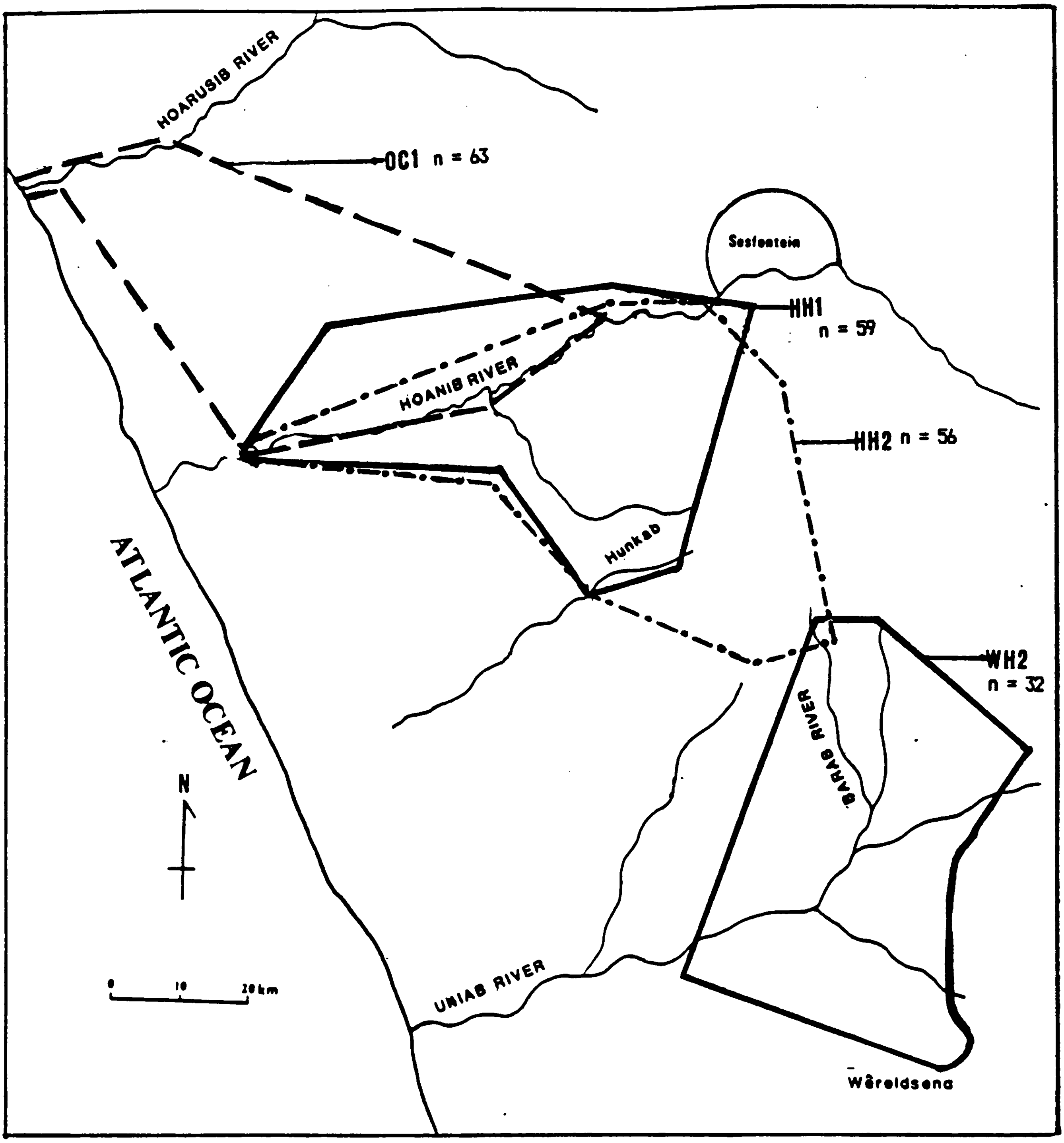


Figure 31: Spatial distribution of adequately defined home ranges for four family groups (OC1, HH1, HH2 and WH2) in the northern Namib Desert region of the Kaokoveld, South West Africa, between 1980 and 1983.

not shown separately in Figure 30. Likewise, the home ranges of family group HH3 was identical to that of HH1 as was HH4 to HH2 and WH1 to WH2. The size, greatest linear dimension, maximum distance between successive locations, number of records and period of observation of the home ranges is presented in Table 14.

Space-use patterns in all home ranges, according to the Poisson distribution, were not at random (χ^2 = 13,2 to 296,5; p<0,01; df=3). This was due to an over-representation of 25 km^2 units containing 2 or more locations. The distribution was obviously also not uniform but showed a clumped distribution pattern. By plotting the smallest portions of each individual's home range that contained at least 25 per cent of all observed locations, two areas of local concentration in each individual home range were identified (Figs. 32 to 37).

In terms of time and space these local concentrations or core areas (Samuel, Pierce and Garton 1985) represented wet and dry season ranges. The combined wet and dry season core areas contained only 19 per cent of the total home range areas but represent 86 per cent of all observed locations in the six home ranges in Table 15. The areas in between (81 per cent of the total home range areas) were used mainly for travelling between the wet and dry season core areas. The dry season core areas were remarkably stable as each given individual elephant returned to exactly the same area in the hot dry season. Wet season core areas were also stable in most home ranges but in others it

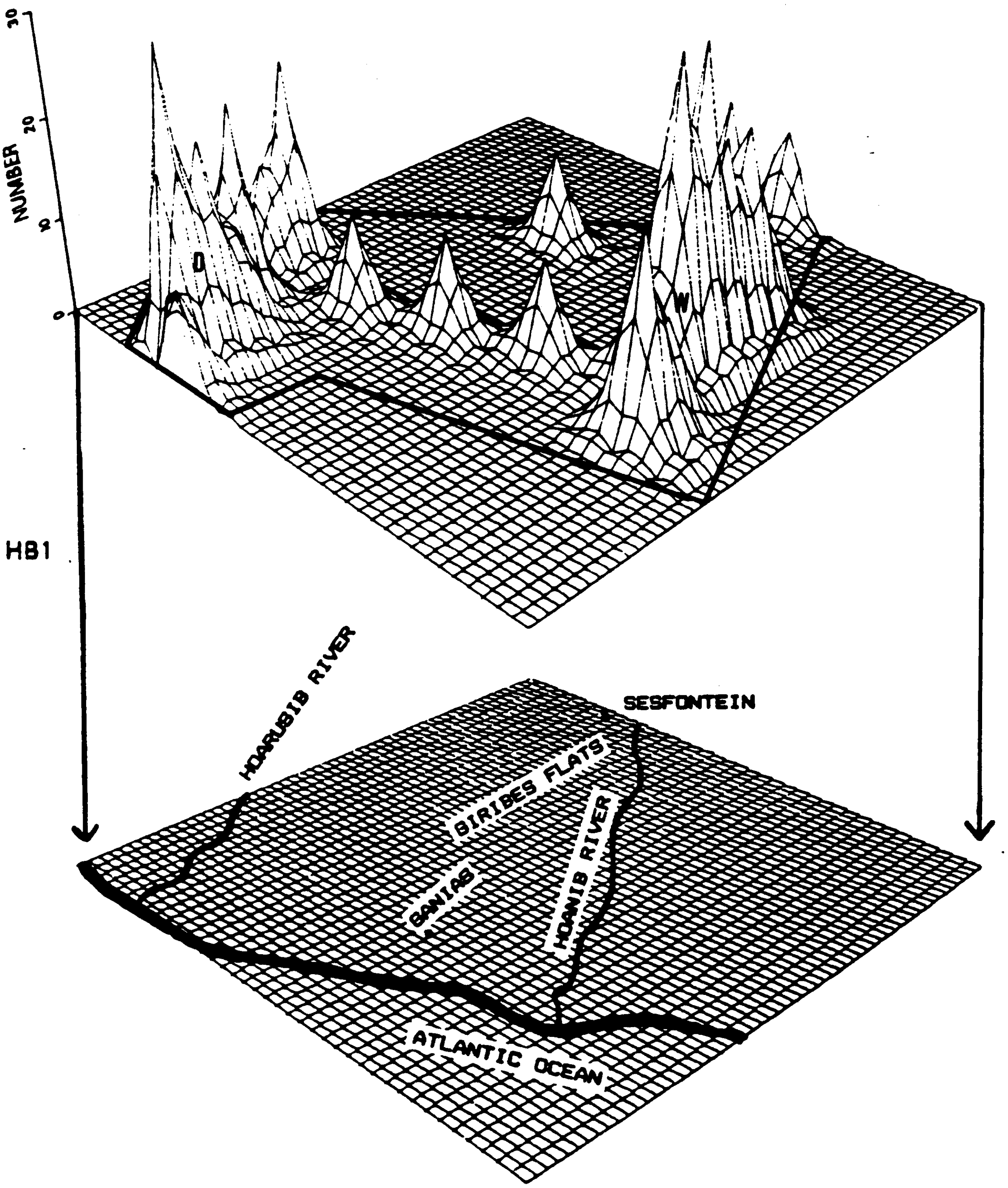


Figure 32: Home range configuration and space-use patterns within the home range of elephant bull 'HB1' in the northern Namib Desert region of the Kaokoveld, South West Africa, between 1980 and 1983. 'D' represents the dry season core area and 'W' the wet season core area.

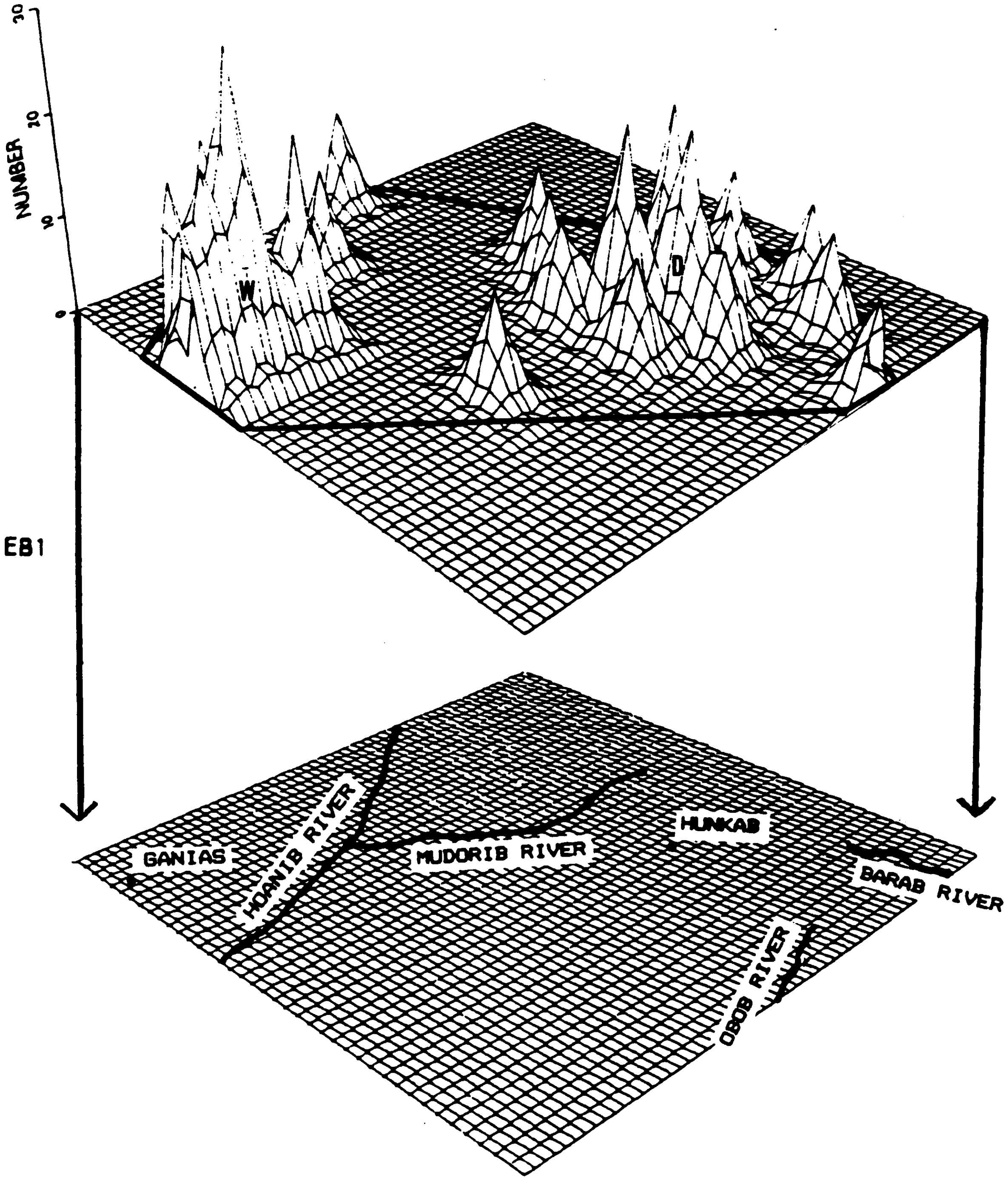


Figure 33: Home range configuration and space-use patterns within the home range of elephant bull 'EB1' in the northern Namib Desert region of the Kaokoveld, South West Africa, between 1980 and 1983. 'D' represents the dry season core area and 'W' the wet season core area.

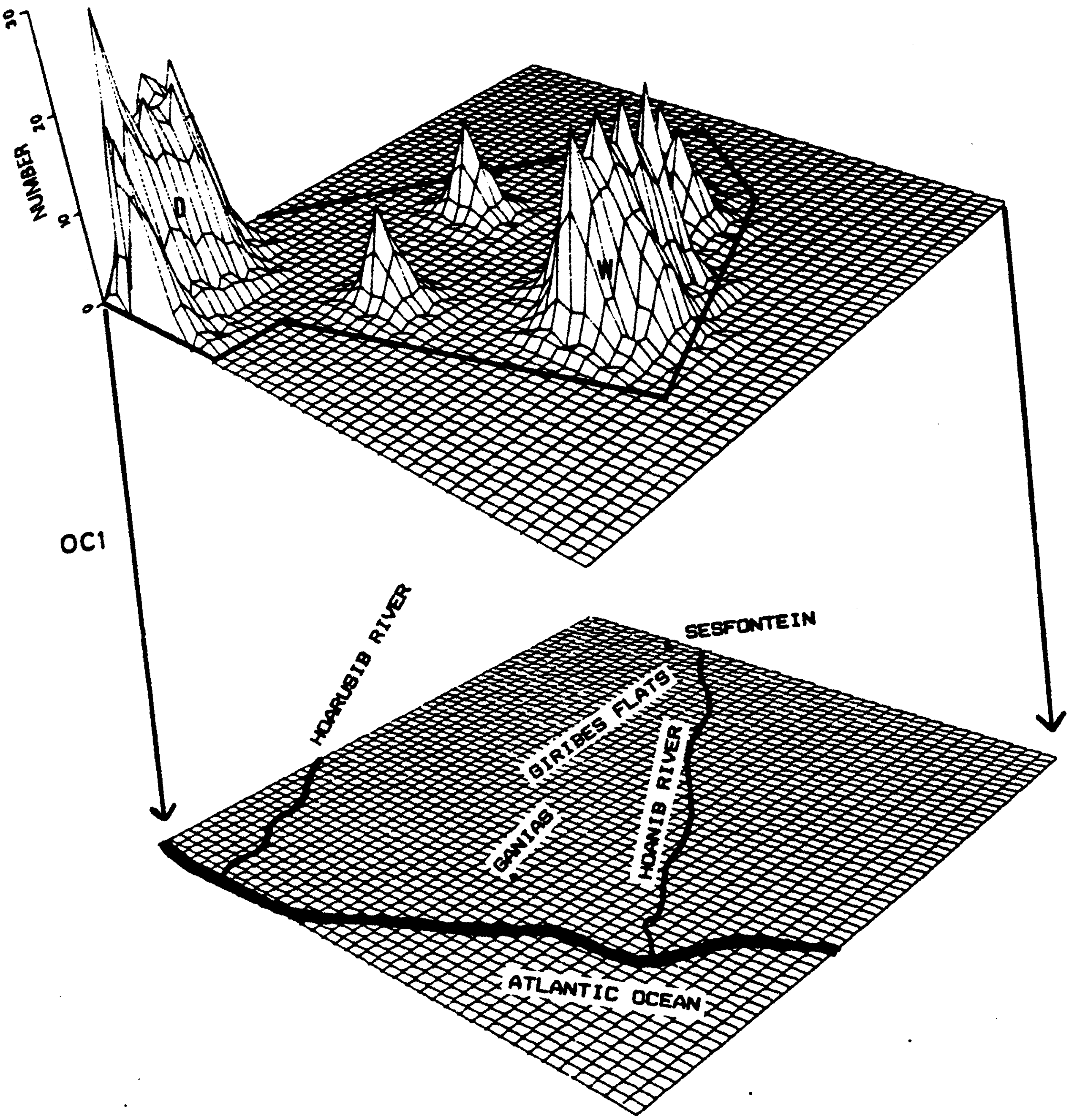


Figure 34: Home range configuration and space-use patterns within the home range of elephant family group 'OC1' in the northern Namib Desert region of the Kaokoveld, South West Africa, between 1980 and 1983. 'D' represents the dry season core area and 'W' the wet season core area.

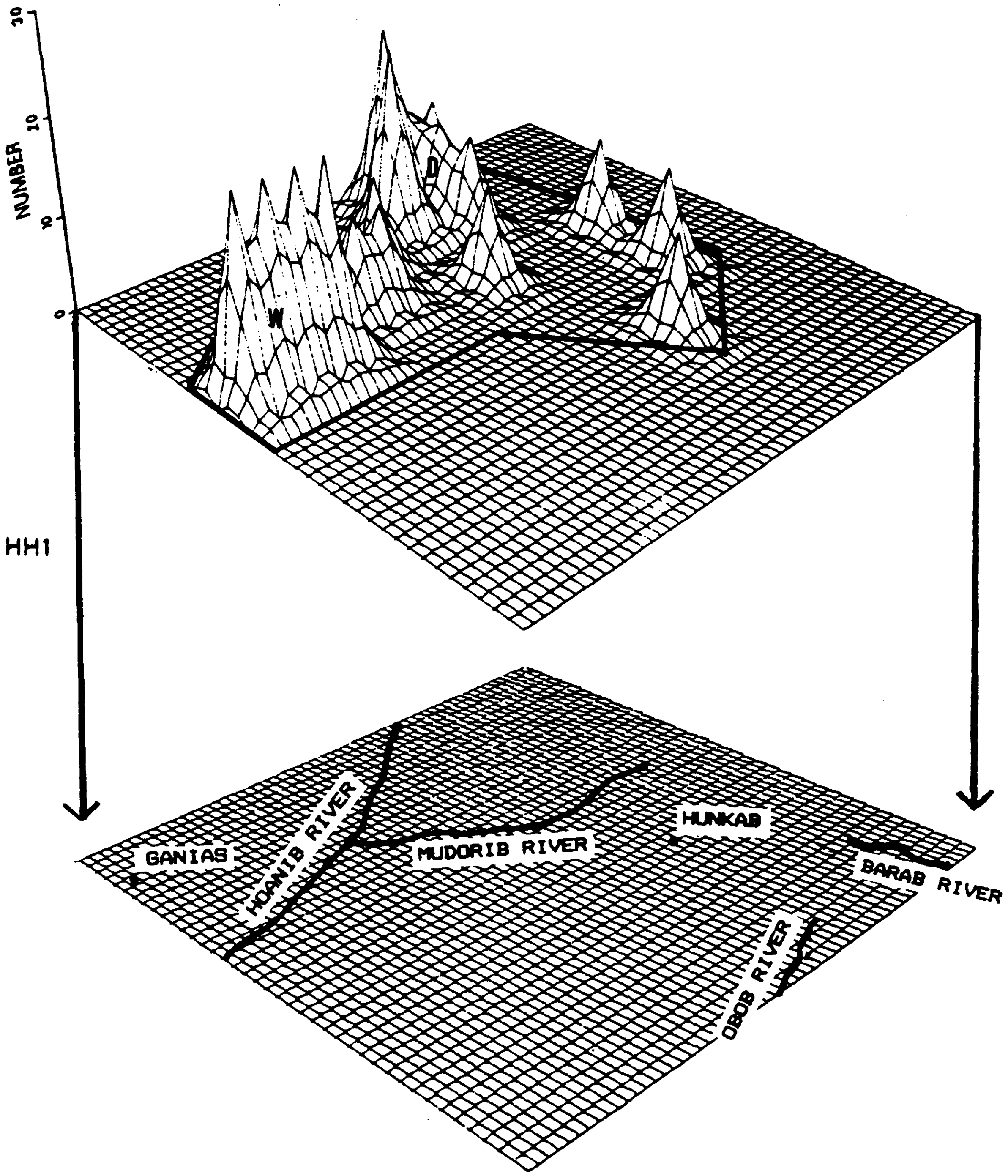


Figure 35: Home range configuration and space-use patterns within the home range of elephant family group 'HH1' in the northern Namib Desert region of the Kaokoveld, South West Africa, between 1980 and 1983. 'D' represents the dry season core area and 'W' the wet season core area.

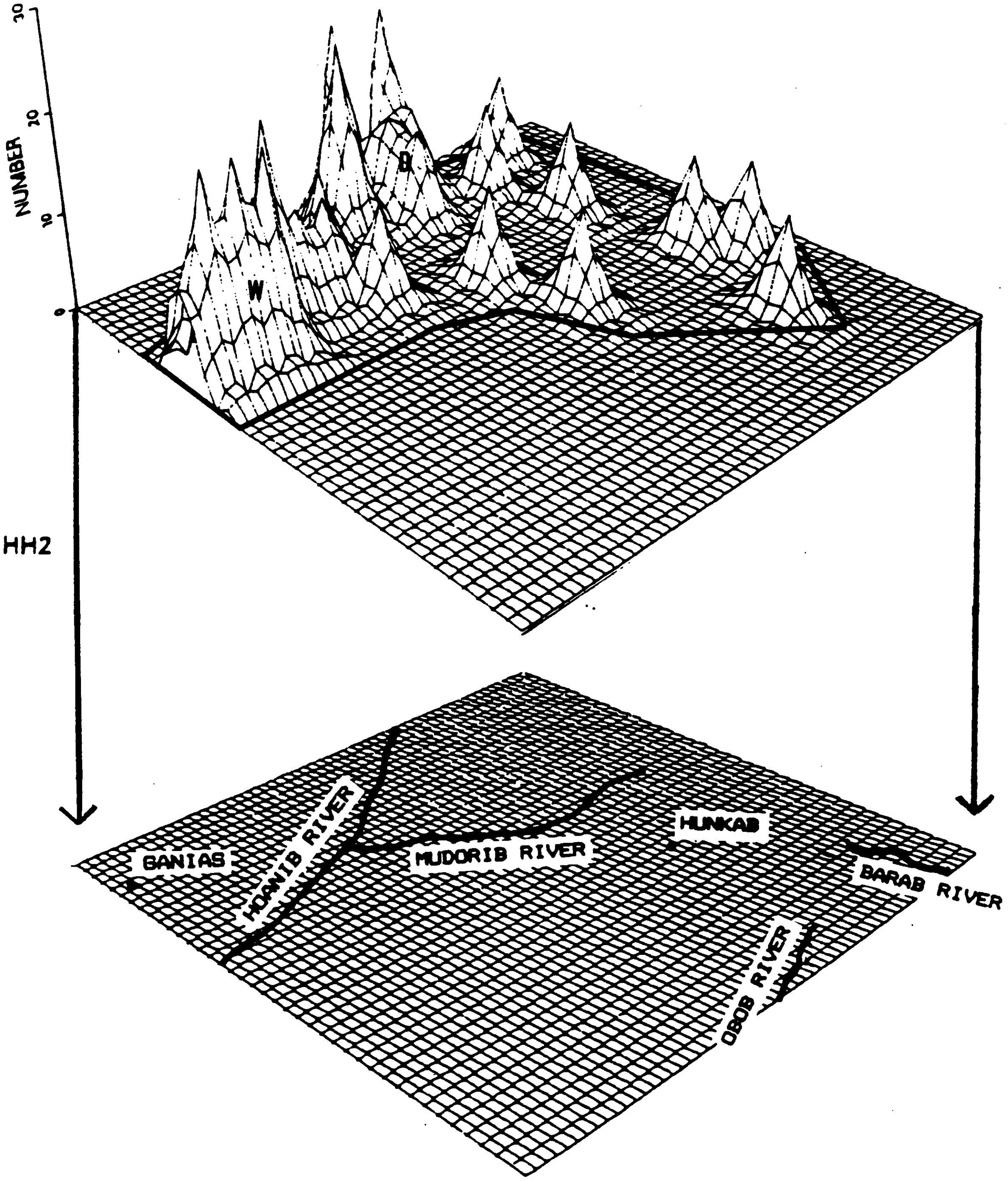


Figure 36: Home range configuration and space-use patterns within the home range of elephant family group 'HH2' in the northern Namib Desert region of the Kaokoveld, South West Africa, between 1980 and 1983. 'D' represents the dry season core area and 'W' the wet season core area.

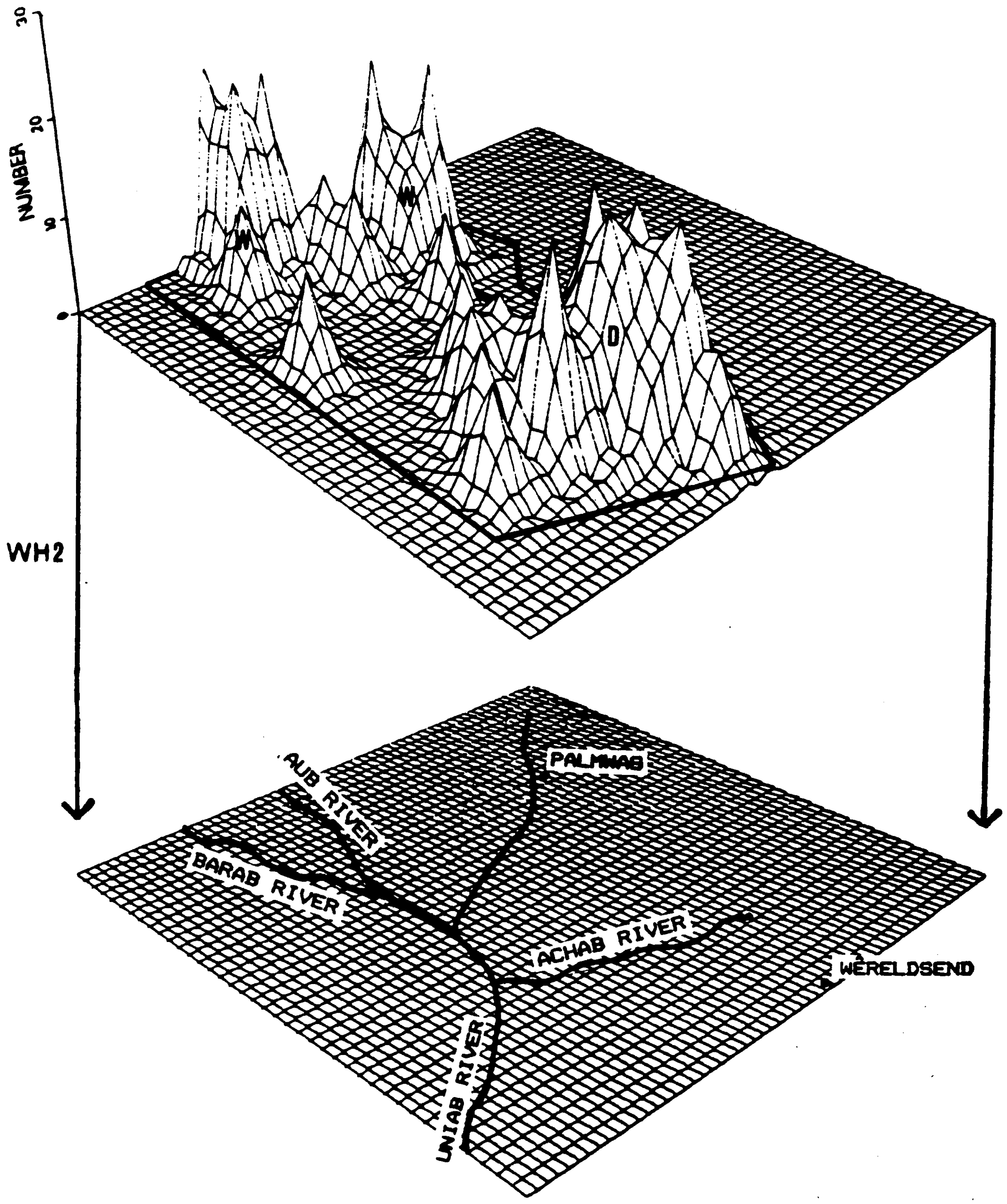


Figure 37: Home range configuration and space-use patterns within the home range of elephant family group 'WH2' in the northern Namib Desert region of the Kaokoveld, South West Africa, between 1980 and 1983. 'D' represents the dry season core area and 'W' the wet season core areas.

Table 15: Summary of data on core areas (km^2) within home ranges of the desert-dwelling elephants of the northern Namib Desert, South West Africa, from 1980 to 1983.

REFERENCE	WET SEASON			DRY SEASON		
NUMBER	Core area	Percentage of home range	Percentage of observations	Core area	Percentage of home range	Percentage of observations
HB1	202,5	6,88	39,3	108,0	3,67	35,7
EB1	190,0	7,26	41,6	393,0	15,62	45,8
OC1	168,5	8,83	27,6	100,0	5,24	58,6
HH1	169,0	9,59	51,7	84,0	4,76	37,9
HH2	162,0	7,98	46,2	267,5	13,17	42,3
WH2	241,0*	13,36	28,6	290,0	16,08	60,7

* Mean size of two different core areas in 1981 and 1982.

appear to vary according to the spatial distribution of rainfall and river floods during the study period. For example, there was a difference between the wet season core areas for the WH1 and WH2 family groups between the 1981 and 1982 seasons. Where home ranges overlapped, core areas were shared by individual bulls or family groups. The dry season core areas all included permanent water supplies, whereas the wet season core areas corresponded to areas of local rainstorms or river floods.

DAILY MOVEMENTS.

Although data were collected separately, the analysis of data on daily distances revealed that there were no significant differences between diurnal and nocturnal movements (Table 16). There were also no significant differences in daily distances moved by the sexes, and in mean daily distance moved in 1981 and 1982. Consequently, all data were grouped to give a larger sample of the distances travelled in a 12-hour period. Figure 38 represents the mean daily movements on a monthly basis as compared to the rainfall and river floods for the same period.

The annual mean distance travelled by the desert-dwelling elephants in a 12-hour period was 12,9 ± 6,43 km (n=79). Between seasons (Fig. 39) there was a significant difference (F=11,86; $P<0,01$; $df_1 = 2$, $df_2 = 71$) in 12-hour distances travelled with the mean distance travelled being at its shortest during the wet season ($\bar{X}$=9,23 ±5,61 km), which gradually increased during the

Table 16: Comparison of different pairs of parameters in distances (km) moved per 12-hour period by the desert-dwelling elephants of the northern Namib Desert, South West Africa, between 1981 and 1982.

PAIR OF PARAMETERS COMPARED	MEAN DISTANCE MOVED	n	SD	CV	RANGE	t-TEST	DF	P
Sexes								
Male	13,44	46	7,04	52,39	4-38	0,13	99	>0,05
Female	13,26	55	6,80	51,29	4-38			
Years								
1981	14,06	27	8,46	60,22	4-38	1,44	72	>0,05
1982	11,74	47	5,18	44,15	4-27			
Time								
Diurnal	12,09	16	9,35	77,28	4-38	-0,40	36	>0,05
Nocturnal	13,19	22	7,05	53,41	5-27			
Seasons								
Wet 1981	9,15	14	5,33	58,22	4-24	-2,12	16	<0,05
Cold 1981	15,50	4	2,35	15,13	13-17,5			
Wet 1981	9,15	14	5,33	58,22	4-24	-4,25	25	<0,01
Hot 1981	20,05	13	7,38	36,82	6-38			
Cold 1981	15,50	4	2,35	15,13	13-17,5	-1,14	15	>0,05
Hot 1981	20,05	13	7,38	36,82	6-38			
Wet 1982	9,29	18	5,82	62,63	4-27	-1,73	32	>0,05
Cold 1982	12,50	16	4,49	35,91	6-18,8			
Wet 1982	9,29	18	5,82	62,63	4-27	-2,69	30	<0,05
Hot 1982	14,19	14	3,53	24,89	5-18			
Cold 1982	12,50	16	4,49	35,91	6-18,8	-1,09	28	>0,05
Hot 1982	14,19	14	3,53	24,89	5-18			

SD= Standard deviation CV= Coefficient of variation DF= Degrees of freedom

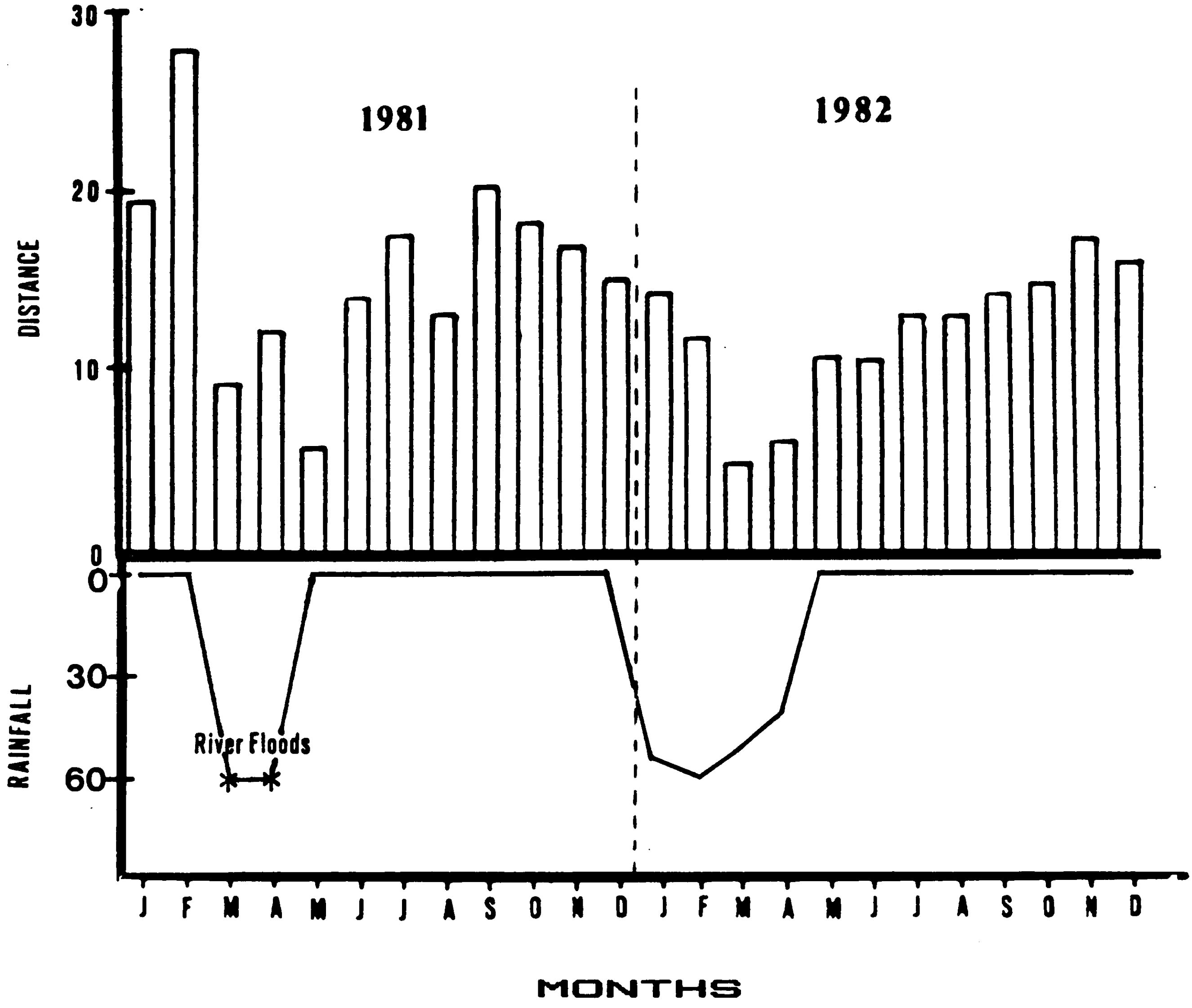


Figure 38: Comparison of mean monthly distance (km) moved in a 12-hour period by the desert-dwelling elephants with rainfall (mm) and the occurrence of river floods in the northern Namib Desert region of the Kaokoveld, South West Africa, during 1981 and 1982.

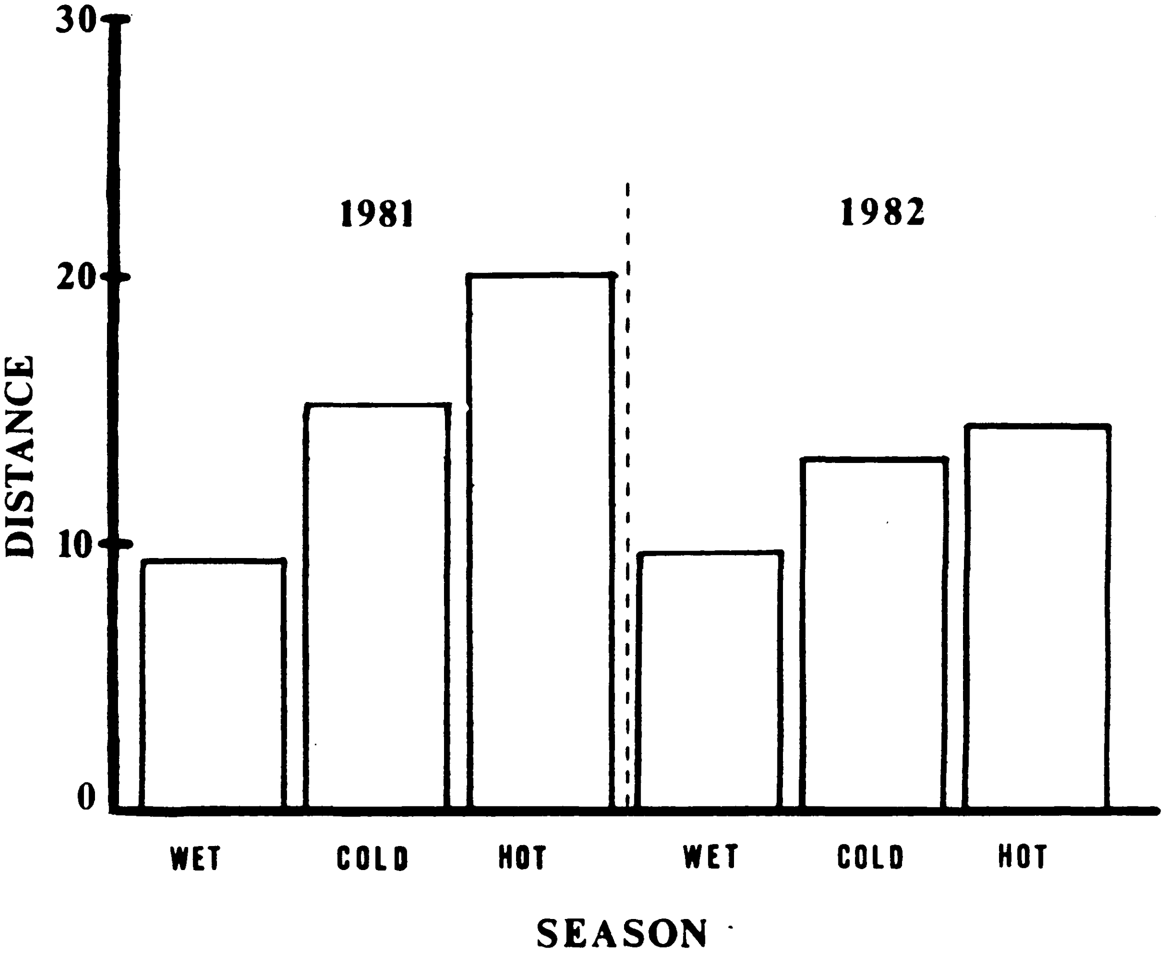


Figure 39: Mean distance (km) moved in a 12-hour period during the respective seasons of 1981 and 1982 by the desert-dwelling elephants of the northern Namib Desert region of the Kaokoveld, South West Africa.

cold dry season ($\bar{X}$=12,6 ±4,86 km) to reach a maximum during the hot dry season ($\bar{X}$=16,9 ±6,67 km). At the onset of the wet season there was an abrupt drop in daily distance travelled following the flush of green vegetation.

During 1981 there were significant differences between the daily distances travelled during the wet season and both the cold dry and hot dry seasons. Distances travelled during the cold and the hot dry seasons did not differ significantly (Table 16). In 1982, however, there were no differences in distances moved in the wet and cold dry seasons, and likewise in the cold and hot dry seasons. Between the wet and hot dry seasons the difference was significant (Table 16).

The daily distances moved by the desert-dwelling elephants were affected by the quality of the available vegetation (green grass) and the proximity of water-holes to the vegetation. This can be illustrated by the following examples:
Between 1977 and 1981 the total yearly recorded rainfall at Sesfontein varied from 31 per cent to 100 per cent below the yearly average of 108,1 mm. In 1982 the total rainfall was 94 per cent above the average. The information on the daily distances travelled by elephants in this study therefore represent both years of extreme drought and abundant rainfall. Even so, the pattern of daily distances moved in both 1981 (dry) and 1982 (wet) was virtually the same (Figs. 38 and 39). This was brought about by the flooding of the dry river beds, when even in 1981 with no recorded rainfall, the major rivers flooded because of

rainfall in the eastern catchment basins. The resultant flooding caused a flush of green vegetation in the river beds and formed temporary water-holes there. However, these water-holes soon dried up. This drying-up is reflected in the abrupt change in daily distances moved between the wet and cold dry seasons of 1981 (Table 16). In 1982, rain fell over a wide area causing an abundance of green grass and temporary water-holes which gradually deteriorated in the cold dry season, a situation which is reflected by the gradual increase in daily distances moved (Figs. 38 and 39).

When comparing rainfall with daily distances moved on a monthly basis, the river floods must also be taken into account, as the effect on the vegetation (although on a smaller scale) in the river courses is the same. For this purpose a value equal to the minimum amount (68 mm) of rainfall needed in the east to cause the rivers to flood, was allocated to that particular month for the study area. Thus, a statistically significant negative linear correlation was found between rainfall and mean monthly daily distances moved ($r = -0,59$; $t=-3,47$; $p<0,01$; $df=23$). However, because the state of the vegetation in a particular month is more likely to be related to the rainfall of the previous month, a stronger negative correlation ($r = -0,64$; $t=-3,93$; $p<0,001$; $df=23$) existed when mean monthly daily distances moved is compared to the rainfall of the previous month in a given area. This correlation is further supported by the short daily distances recorded in May ($\bar{X} = 9,19 \pm 5,62$ km) when no rainfall actually occurred, but when the effect of the rainfall on the vegetation and temporary water-holes in close proximity to each other was maximal.

The extremely long daily distances moved during January and February 1981 was a direct result of the elephants' usual water-holes drying up, which forced the elephants to utilize water-holes far removed from their food resources. It is during this period that an elephant's drought tolerance was tested to the utmost and it also was the period in which 80 per cent of the other game in the Kaokoveld died as a result of this drought (Viljoen 1982b). The ability of the elephants to move long distances between food and water probably saved them from a similar fate.

SEASONAL DISTRIBUTION

Figures 40 to 45 show the seasonal distribution patterns of the desert-dwelling elephants for 1981 and 1982, thus representing a year with no rainfall and a year with an abundance of rainfall. Elephants were aggregated in all seasons and their distribution departed significantly from randomness (Poisson distribution: $\chi^2 =$ 46,44 to 240,58 ; $p < 0,001$; df=7). Corresponding seasons in both years showed similar patterns and the observed differences are related to the pattern of rainfall and river floods in the respective years.

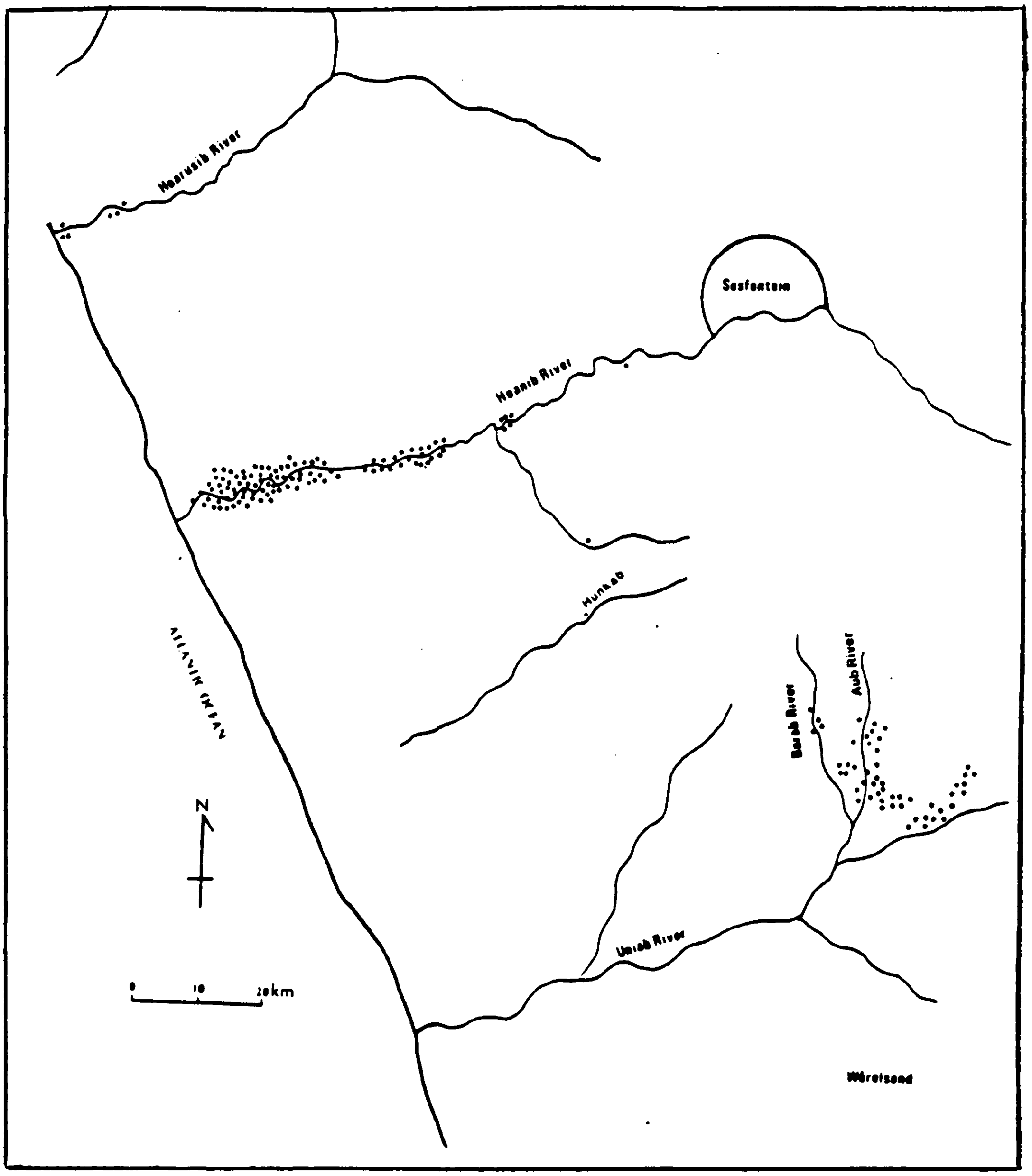


Figure 40: The 1981 wet season distribution of the desert-dwelling elephants in the northern Namib Desert region of the Kaokoveld, South West Africa. Each dot represents one elephant.

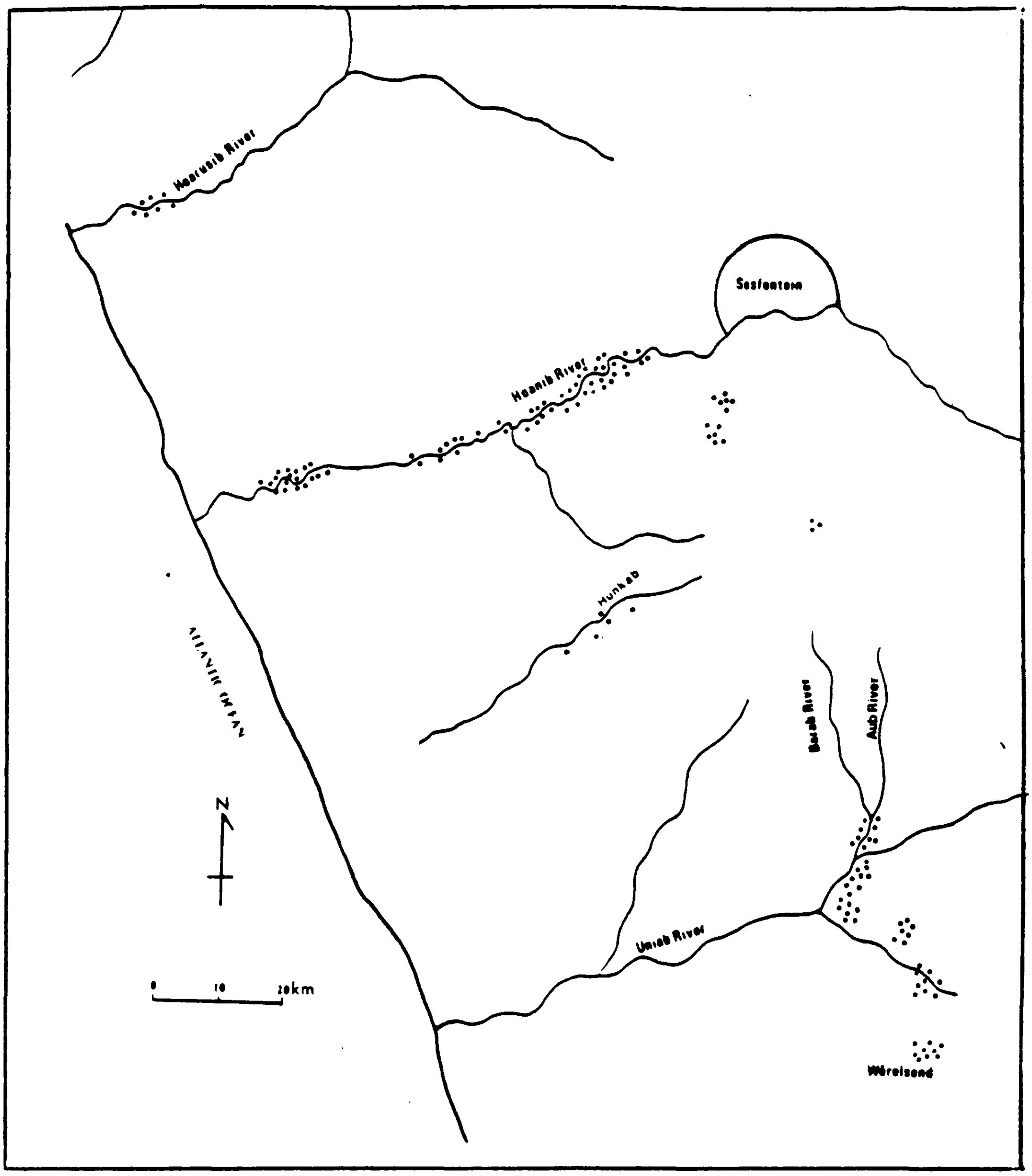


Figure 41: The 1981 cold dry season distribution of the desert-dwelling elephants in the northern Namib Desert region of the Kaokoveld, South West Africa. Each dot represents one elephant.

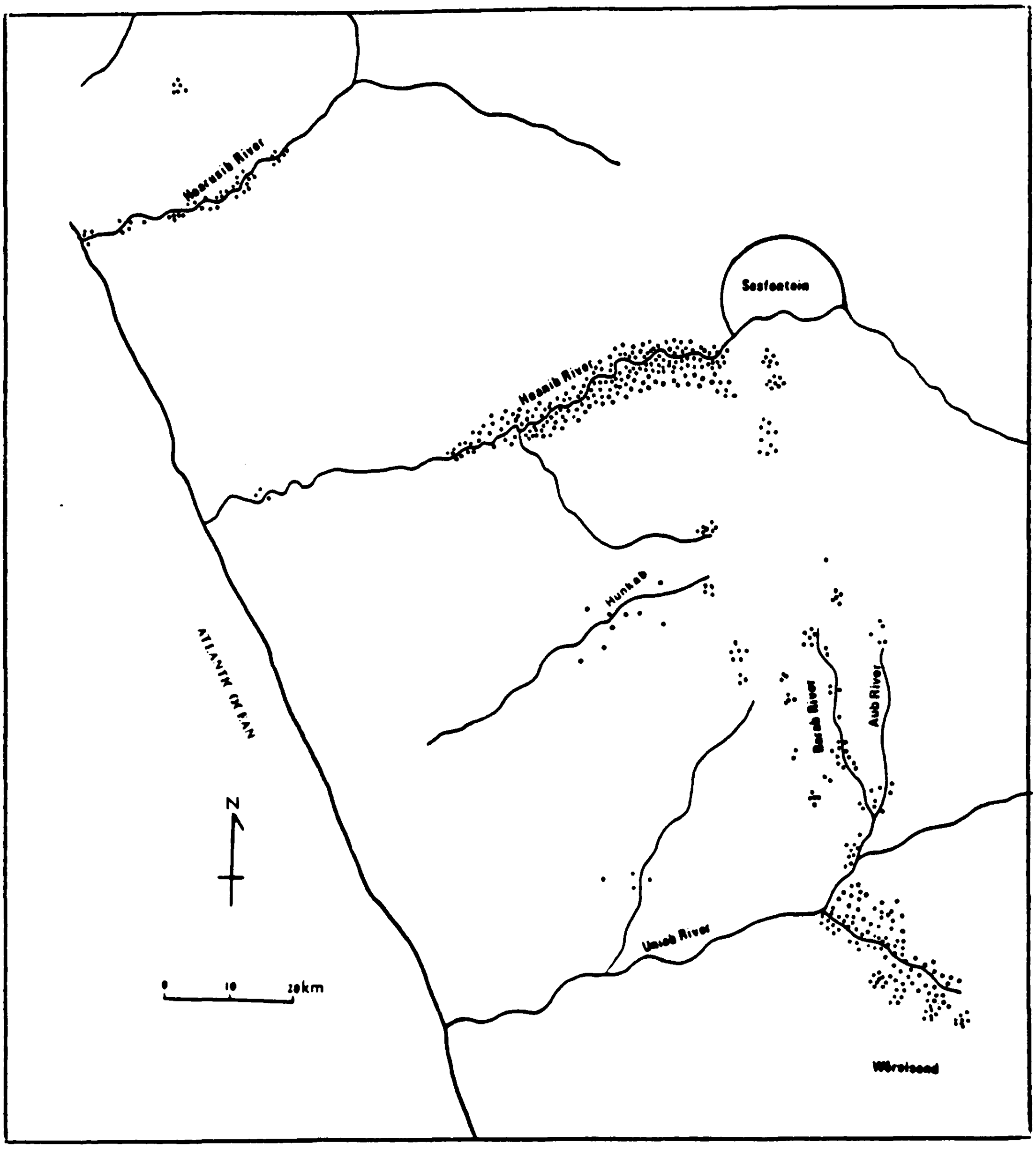


Figure 42: The 1981 hot dry season distribution of the desert-dwelling elephants in the northern Namib Desert region of the Kaokoveld, South West Africa. Each dot represents one elephant.

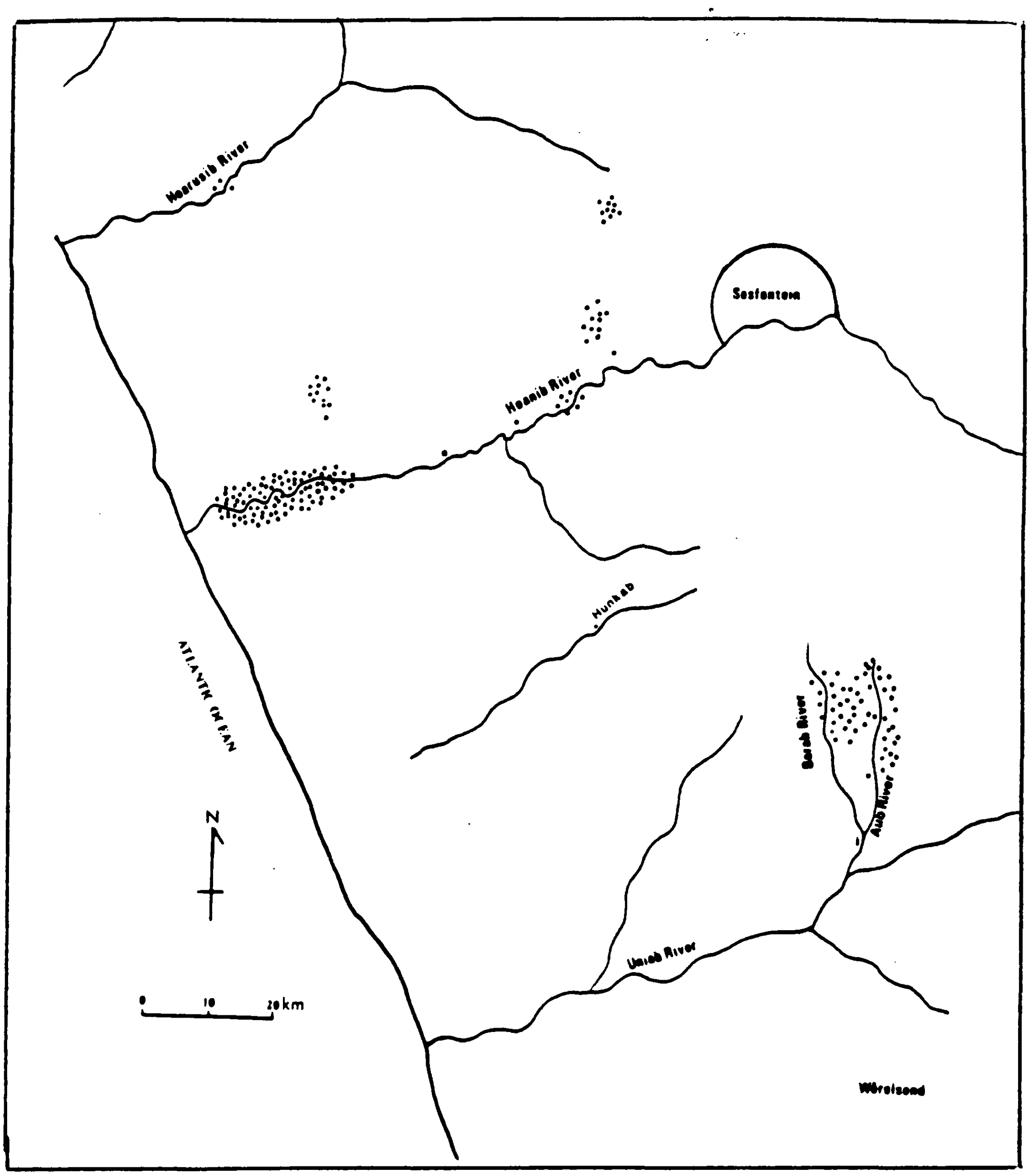


Figure 43: The 1982 wet season distribution of the desert-dwelling elephants in the northern Namib Desert region of the Kaokoveld, South West Africa. Each dot represents one elephant.

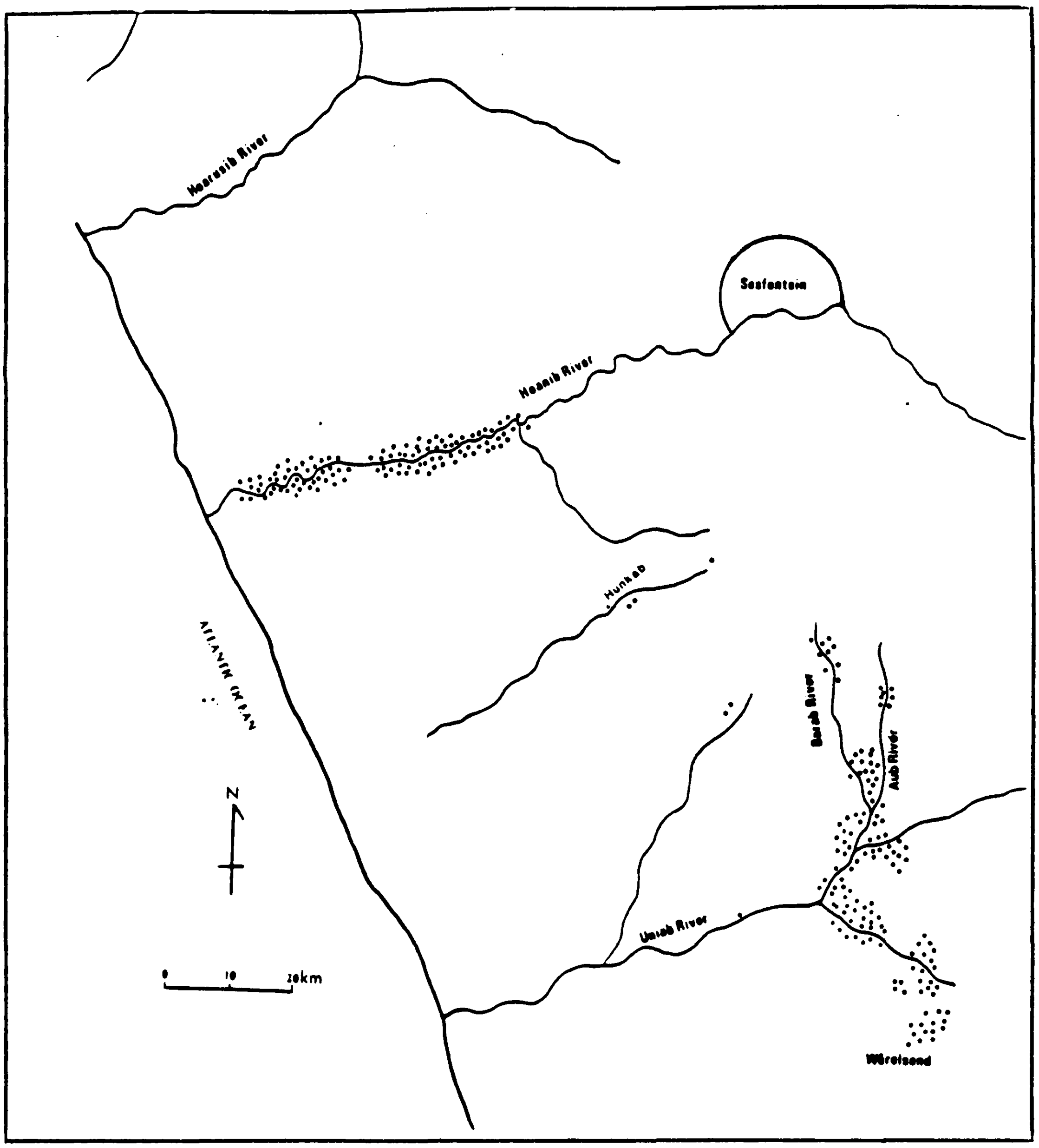


Figure 44: The 1982 cold dry season distribution of the desert-dwelling elephants in the northern Namib Desert region of the Kaokoveld, South West Africa. Each dot represents one elephant.

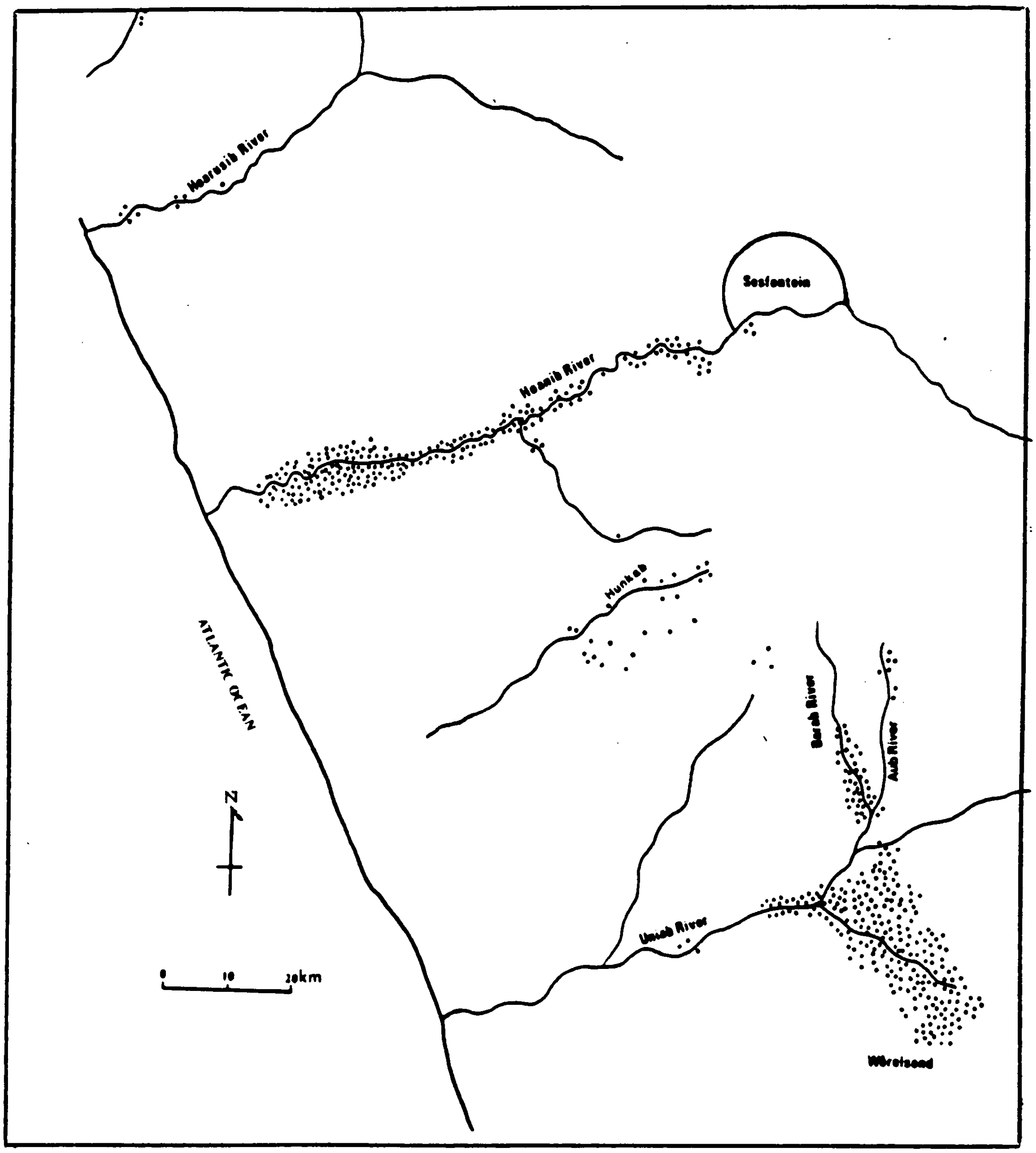


Figure 45: The 1982 hot dry season distribution of the desert-dwelling elephants in the northern Namib Desert region of the Kaokoveld, South West Africa. Each dot represents one elephant.

In the hot dry seasons, elephants were essentially restricted to areas with permanent food and water supplies. This was well illustrated in the 1981 hot dry season (Fig. 42), when the elephants concentrated at permanent water-holes in the vicinity of the Wêreldsend, Hunkab, and the Hoanib River and Hoarusib River areas. In 1982 (Fig. 45), after widespread rains in the previous wet season, elephants tended to remain in areas where temporary water-holes and green plants lasted into the hot dry season, e.g. the western course of the Hoanib River and the lower reaches of the Barab River.

Distribution during the wet season was influenced by localized rain showers and/or river floods. For example, during 1981 (Fig. 40) virtually all the elephants moved to either the western Hoanib River flood plain or the vicinity of the Aub River, depending on their individual home ranges. The movement to the Aub River apparently was triggered by a localized rain shower in that vicinity. The concentration of elephants in the western Hoanib River flood plain was initiated by river floods, resulting in an abundance of green grass and an accumulation of water in this region. In the 1982 wet season (Fig. 43), the pattern was repeated with the exception of a shift in distribution from the Aub River to the upper reaches of the Barab River, reflecting the distribution of maximum rainfall in the area (as was evident from the vegetation growth in the area). The additional forays north of the Hoanib River, reflected the widespread rainfall in that area although the main concentration of elephants was still in the flood plains which had an abundance of green grass.

The distribution patterns in the cold dry season (Figs. 41 and 44) illustrate an intermediate movement between the wet and hot dry season ranges, a period when the elephants start to move back from the wet season ranges to their respective hot dry season ranges. This was brought about by the gradual dwindling of temporary water and food supplies in the wet season ranges.

LONG-DISTANCE MOVEMENTS

Figure 46 depicts the pattern of the long-distance movements of the desert-dwelling elephants between between October 1980 and January 1983. The long-distance movements ranged from 31 to 195 km and the observed monthly frequency of all long-distance movements deviates significantly from an assumed even distribution throughout the year ($\chi^2 = 49,45$; $p < 0,001$; df=11). Twenty-five (40,3 per cent) of the 62 long-distance movements summarized in Table 17 took place in January and February, i.e. near the wet season and following the hot dry season. A second peak (19,4 per cent) occurred at the end of the wet season (May and June).

Long-distance movements by bulls occurred mainly between November and February (65 per cent of all bull movements) while family

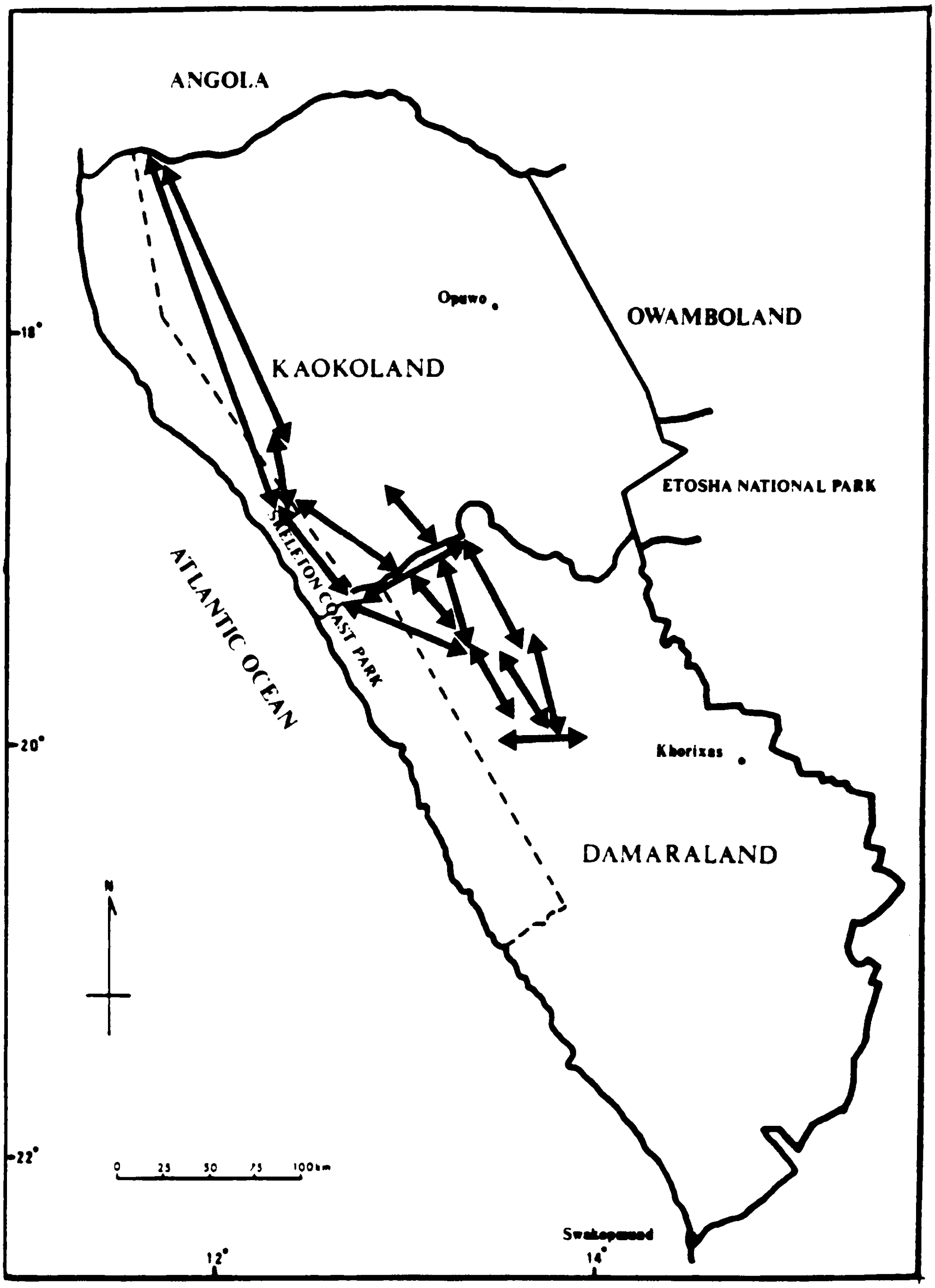


Figure 46: Patterns of long-distance movements (arrows) by the desert-dwelling elephants between 1980 and 1983 in the northern Namib Desert region of the Kaokoveld, South West Africa.

Table 17: Summary of the mean, standard deviation and range of long-distance movements (km) by visually identifiable desert-dwelling elephants in the northern Namib Desert, South West Africa, between 1981 and 1983.

MONTH	MEAN	SD	RANGE	FREQUENCY	DISTANCE CLASS INTERVAL			
					31-40	41-50	51-60	>60
January	58,8	8,58	39-74	6	1	0	4	1
February	47,6	15,22	31-90	19	7	5	4	3
March	39,0	0,00	39	1	1	0	0	0
April	67,3	2,31	66-70	3	0	0	0	3
May	43,0	14,04	31-66	8	6	0	0	2
June	78,5	52,22	38-155	4	1	0	1	2
July	56,3	17,56	38-73	3	1	0	1	1
August	52,2	14,41	31-74	6	1	1	3	1
September	49,0	0,00	49	1	0	1	0	0
October	49,7	20,20	38-73	3	2	0	0	1
November	92,4	61,53	38-195	5	1	0	1	3
December	54,0	20,81	41-78	3	0	2	0	1
Total	55,5	27,19	31-195	62	21	9	14	18

groups showed a preponderance of long-distance movements from January to May (59 per cent of all family group movements).

Five of the observed 62 long-distance movements were well outside the individual elephant's home range. These movements were regarded as wanderings as they occurred infrequently and were not repeated regularly. The longest of these wanderings was that of the family group of elephants that frequented the Kunene River area: In October 1981 they moved south to the Hoarusib River; a straight line distance of 195 km. This was followed in July 1982 by a movement of 155 km by the same group to the Khumib River. Wanderings, however, were of short duration and all wanderings observed (n=5), lasted less than 20 days, after which the individual elephants concerned returned to their original home ranges. All other long-distance movements occurred within individual home ranges as previously defined.

WATER-RELATED MOVEMENTS AND DRINKING FREQUENCIES

The mean distance (n = 47) that the desert-dwelling elephants was observed from the nearest water point during the 1981 hot dry season was 25,7 ± 13,2 km. The maximum distance that elephants were observed from the nearest water point was 70 km. Most of the observations of elephants (57,4 per cent) were between 20 and 40 km from the nearest water point, while 12,8 per cent of the elephants were located more than 40 km from the nearest water point. Only 29,79 per cent of the locations were less than 20 km from the nearest water-hole. From the above data it would appear that the elephant's normal feeding grounds (in which they spent most of their time) during the dry season was between 21 and 40 km from the nearest water. In the wet season this distance was reduced to a radius of less than 15 km from the nearest water-hole where all observations were made.

The above information agrees with the observed drinking frequencies of the desert-dwelling elephants: During the hot dry season the period between drinking sessions varied between 48 and 96 hours (n = 17), with six observations of 48 hours between sessions, five of 72 hours and six of 96 hours. During the wet season the period between drinking sessions varied between 19 and 36 hours (n = 10), with eight observations of 24 hours apart, one of 19 hours and one of 36 hours. Only those observations were there was no doubt as to the drinking frequency of the elephants were considered. Because the observations were not done on a continuous basis, it was considered invalid to calculate mean drinking frequencies. From the above it would appear that during periods of an abundance of water, the desert-dwelling elephants normally drink water only once in 24 hours. During the hot dry season, when permanent water supplies are far removed from the feeding grounds, the elephants are able to extend their drinking intervals as necessity dictates to up to 96 hours.

DISCUSSION

HOME RANGE

The presented data on elephant home range size indicate that at least 18 to 24 months of observations are required to reach an asymptote which would provide a reasonable indication of a given elephant's actual home range. Home range sizes obtained for shorter periods must be considered as provisional.

The spatial distribution and sizes of adequately defined individual home ranges in the northern Namib Desert indicate that individual home ranges overlap considerably, both among family groups and between sexes. Home ranges of male elephants are significantly larger than those of family groups, illustrating the greater mobility of bulls as opposed to family groups. The linear dimensions of the home ranges indicate that north-south movements within the home ranges are prominent with the exception of the Hoanib River area where the movements are mainly east-west. All home ranges are restricted to the same bioclimatic region. Even though the elephants moved over considerable distances of up to 97 km for bulls and 75 km for cows, these movements never extended east of the 150 mm isohyet. Also, occasional wanderings outside the home ranges, were always north-south orientated, and still stay within the original bioclimatic zone occupied as home range. Based on the spatial distribution of the home ranges and the extent of overlap, the elephant population can be divided into two, possibly three, groups or clans (Chapter 4): a group that frequents the Wêreldsend-Obob area in the south-east of the study area and a group that frequents the Hoarusib-Hoanib-Hunkab areas. The Kunene River area is frequented by a third group of which the home range is not adequately defined. Although home ranges within the same group overlap considerably in area (>80 per cent), those of adjacent groups overlap to a lesser extent (<30 per cent). Core areas comprise a relatively small area of each individual home range. Dry season core areas appear immutable while wet season core areas tend to vary according to rainfall and river floods.

Home range sizes for elephant in other regions in Africa indicate that an elephant's home range varies to a great degree in different habitat types. For example, in the Lake Manyara area, with an annual rainfall of 380 to 1270 mm, the elephants' home ranges vary between 14 and 52 km^2 (Douglas-Hamilton 1972). Leuthold (1977) on the other hand recorded a mean home range of 746 km^2 for the elephants in Tsavo-West (annual rainfall = 260 mm) and 1620 km^2 in Tsavo-East (annual rainfall = 550 mm). Merz (1986) recorded elephant home ranges of between 210 and 290 km^2 for the forest elephants in the Gola Forest Reserve (annual rainfall = 2800 - 3200 mm). In the Middle Zambezi Valley, Zimbabwe, with an annual rainfall of 783 to 802 mm, Dunham (1986) reported home range sizes of between 94 and 263 km^2 for cows.

The home range sizes of the desert-dwelling elephants are considerably larger than any of those mentioned above (mean =

2172 km^2). These differences probably in part reflect the type and quality of the habitat as the northern Namib Desert only receives from 19,0 - 108,1 mm of rain per year; considerably less than that of any of the above-mentioned areas.

DAILY MOVEMENTS

Although there are few studies which are directly comparable, the overall mean distance of 25,7 km moved by the desert-dwelling elephants in 24 hours during this study is further than that of most other elephant populations studied thus far. Young (1970), who plotted the actual meandering courses of elephants in the Kruger National Park, reported that those elephants moved a mean daily distance of 17,4 km per 24 hours in the summer and 8,3 km in the winter. De Villiers (1981) reported that the elephants in the Etosha National Park moved from 3,0 to 14,5 km in 24 hours. In some studies, (i.e. Wyatt and Eltringham 1974 and Barnes 1982), the daily movements of elephants were recorded in distances moved per hour. Extrapolations suggest that distances moved over 24 hours range from 2,4 km to 18,5 km. Williamson (1975), reported daily movements of up to 32 km in the wet season and 24 km in the dry season for the elephants of the Wankie National Park. However, from Williamson's (1975) information these movements seemed to involve maximum distances moved instead of mean daily movements. The data in the present study on daily movements are not comparable to that of Douglas-Hamilton (1971), Leuthold (1977) and Fairall (1979) since they recorded straight-line distances between radio fixes. These distances varied from 0,4 to 21,4 km over 24 hours.

The longer daily distances moved as recorded for the desert-dwelling elephants during the hot and cold dry seasons were directly related to increased distances between available food and water. As the dry season progressed the temporary water-holes dried up. The food in the immediate vicinity of the permanent water-holes was consumed first, with the result that the elephants thereafter had to move increasingly further away from the water to satisfy their food requirements. As the elephants, however, usually returned to the same water-hole, the actual shifts in position during the dry seasons were relatively small. In contrast, during the wet season, the elephants roamed between several temporary water-holes over a large area. Thus although their daily distances moved were relatively short, the actual shift in position over a period of time was larger than that during the dry seasons. This explains the discrepancy observed between the results of the present study and those of Douglas-Hamilton (1971) and Leuthold (1977), who reported shorter daily movements in the dry season. In these latter studies daily shifts in positions were recorded rather than daily distances moved since it were calculated by dividing the linear distance between two locations by the number of days between successive radio fixes. However, the discrepancy of the current data with that of Young (1970) cannot be explained. The shorter distances moved in the Kruger National Park in the dry season may possibly be influenced by the distribution of artificial water-holes in the

Kruger National Park.

The ability of elephants to move over long distances is not unique to the desert-dwelling elephants and there are many reports of elephants in other populations which occasionally travelled long distances (Wing and Buss 1970, Sikes 1971, Leuthold and Sale 1973, Laws et al. 1975, Leuthold 1977, De Villiers 1981). However, the ability of the desert-dwelling elephants to travel such long daily distances (25,7 km) regularly, might be unique and conceivably acquired through selective pressures. This ability must be one of the important factors in the survival of these elephants in the desert. In 1981, when most of the desert-adapted herbivores (Louw and Seely 1982) such as the gemsbok Oryx gazella and the springbok Antidorcas marsupialis, died from a lack of food in the vicinity of the water-holes, the elephants used their ability to range over long distances to utilize the remaining food sources far from the available water sources. The result was that not one of the desert-dwelling elephants died during the drought. This was in contrast to the elephants in eastern Kaokoveld, where at least five elephants died as a result of the same drought. Also, during the same drought, approximately 200 elephants died in the Etosha National Park, presumably from anthrax, but nutritional stress may have been the proximate cause (Berry and De Villiers 1982).

SEASONAL DISTRIBUTION

The aggregated seasonal distribution of the desert-dwelling elephants reflected the spatial distribution of food and water resources which is not uniformly distributed in the northern Namib Desert. Wet season movements were apparently triggered off by rain showers or river floods as the transition from the hot dry season range to the wet season range was sudden in contrast to the gradual movement back to the hot dry season ranges. The hot dry season ranges were fixed, but the wet season ranges could differ in response to rainfall distribution. In agreement with Laws (1970), Kerr and Fraser (1975), Leuthold (1977) and Western and Lindsay (1984), seasonal movements in the present study were generally confined to individual home ranges and, following the wet season movements, elephants returned to the same area each dry season. There was an apparent fidelity to individual seasonal ranges, in correspondence to their individual home ranges because irrespective of rainfall or river floods in adjacent areas, individual elephants restricted themselves to their respective seasonal ranges.

Seasonal changes in the distribution of elephants has been well documented (Buss and Savidge 1966, Watson and Bell 1969, Leuthold and Sale 1973, Smuts 1974, Caughley and Goddard 1975, Kerr and Fraser 1975, Laws <u>et al.</u> 1975, Williamson 1975, Eltringham 1977, Leuthold 1977, Western and Lindsay 1984) and coincide with seasonal climatic changes and the corresponding changes in food and water availability. This seasonal use of habitat is probably an important mechanism of survival and optimum utilization of resources, while at the same time reducing the impact on the dry season ranges.

LONG-DISTANCE MOVEMENTS

Long-distance movements of the desert-dwelling elephants showed a marked preponderance of north-south over east-west movements, the latter being virtually confined to the Hoanib River area. In many cases the long-distance movements occurred during seasonal migrations in response to local rainfall or river floods. Other movements could be related to dwindling food and water supplies during the hot dry seasons. However, some of the elephants' movements or wanderings could not be explained adequately.

The preponderance of long-distance movements at the beginning of the wet season illustrates the still unexplained ability of elephants to sense local rain showers or river floods over considerable distances, even against the prevailing winds. Elephants were observed at the location of a recent flood or rain shower within three days after the occurrence of rain or floods.

Since the long-distance movements represent monthly shifts in distribution (measured as straight line distances between successive monthly locations) rather than actual distances travelled , the second peak at the end of the wet season illustrates the roaming of the elephants between temporary water and food sources over a wide area although their actual daily meandering courses were of limited extent.

A striking feature of all movements, including wanderings, is that all were confined to that area of the Kaokoveld west of the 150 mm isohyet. None was observed to extend east of this invisible line. The suggested migration by the desert-dwelling elephants to and from the Etosha National Park (Bigalke 1958, Tinley 1971, Woods 1973), could not be confirmed during the present study. In fact, the elephants showed a marked disposition to remain within their individual home ranges west of the 150 mm isohyet. Nearly all movements (92 per cent) were concentrated within the home ranges, even in times of extreme drought (Chapter 2). During the entire study period no elephant emigration or immigration occurred in the northern Namib Desert.

Although the elephant is regarded as a mobile animal, there are few authentic records of long-distance movements or migrations by elephants. In the absence of reliable data, there have been many speculations about the movements of elephants, and migrations of up to 640 km are quoted (Roberts 1951, Dorst and Dandelot 1970, Sikes 1971). The longest definitely known movements reported are up to 185 km (Wing and Buss 1970, Leuthold 1977, De Villiers 1981), but these movements were considered to be occasional wanderings by individuals and cannot be classified as migrations. Detailed investigations, such as those of Laws (1969a, 1970), Douglas-Hamilton (1972), Leuthold (1977) and the present study revealed that elephant movements are normally local, and generally confined to the respective home ranges. There are no evidance of mass population migrations. However, there can be no doubt that elephants are able to move extremely long distances as their occasional appearances in areas far from their normal ranges proves (Von Moltke 1945, Smithers 1971, Skead 1980).

WATER-RELATED MOVEMENTS AND DRINKING FREQUENCIES

It is generally accepted that water availability and distribution are the most important factors affecting or limiting year-round elephant distribution (Laws 1970, Poche 1974, Smithers 1971, Weir 1972, Kerr and Fraser 1975). Most authors reported that elephants move a maximum distance of between eight and 24 km from the nearest water supply (Laws 1970, Young 1970, Kerr and Fraser 1975, Williamson 1975, De Villiers 1981). In most studies it was also found that elephants drink regularly on a daily basis or even more often (Laws 1970, Smithers 1971, Poche 1974, Wyatt and Eltringham 1974, Guy 1976, Hanks 1979, De Villiers 1981), the exception being the elephants of the Kruger National Park where Young (1970) observed a mean drinking interval of 43,4 hours. However, it is also generally agreed that elephants are capable of going for long periods without water and a maximum of up to 72 hours is known (Young 1970, Smithers 1971, Poche 1974, Wyatt and Eltringham 1974).

In the northern Namib Desert region of the Kaokoveld, however, the elephants as a rule moved further away from water and also had longer drinking intervals than elephants in other parts of Africa. Again, this is also a reflection of the climatic regime and distribution of water and food supplies in the northern Namib Desert. Important, however, is the desert-dwelling elephant's apparent ability to make maximum use of their natural capabilities on a regular basis (e.g. mobility and extended drinking intervals), resulting in a highly flexible survival strategy. During periods of abundance (wet season), the elephants reduced both their drinking intervals and the distance ranged away from water, but during drought conditions the elephants were able to extend both facets with no apparent ill effects. This strategy made these elephants less dependent on the proximity of water in relation to food distribution than other large mammals in the northern Namib Desert like the gemsbok (Viljoen 1980).

EVALUATION OF MOVEMENT STRATEGIES

The main feature of the desert-dwelling elephants' spatial distribution, is their marked fidelity to individual home ranges. These home ranges seem to be immutable and knowledge of them seems to be maintained by tradition within each tightly knit family group or even between individual bulls. This has also been observed in other elephant populations in Africa (Wyatt and Eltringham 1974, Leuthold 1977). Knowledge about resource distribution within the home range, as illustrated during the present study by movements between core areas where elephants head unerringly towards isolated water-holes after an absence of more than eight months, must be an important key in the survival of the elephants in the desert. Haphazard wanderings cannot take place as some water-holes are more than 60 km apart, and to miss such a water-hole would be fatal to any wandering elephant.

Without an intimate knowledge of the location of the widely scattered water-holes and food resources it is doubtful if any elephant will survive for long in the desert. This probably explains the elephants' reluctance to leave individual home ranges, even if more favourable conditions develop in adjacent areas. Unfortunately, this fidelity to their home ranges has caused the destruction of entire elephant herds in the past when their reluctance to leave their home ranges in the face of heavy hunting pressure has led to their deaths as discussed previously. Inadvertently, however, the extermination of entire herds provides further proof of the attachment of such elephants to their individual home ranges. Vacant areas thus created, as in the Hoarusib River east of Leylandsdrift, remain vacant in spite of an overabundance of food and water and the presence of elephants in adjacent areas. No cases were found of elephants moving permanently into new ranges as a result of hunting or other pressures. Thus while fidelity to a home range is a key factor in their survival in the desert, it also proved fatal in the presence of human intervention.

While the elephants undertake extensive movements within a large home range, no regular migrations outside these home ranges were detected. This spatial strategy is in agreement with the observations in other detailed elephant studies, such as those of Laws (1970), Douglas-Hamilton (1972), Wyatt and Eltringham (1974), Laws _et al._ (1975) and Western and Lindsay (1984), but it lends no support for reports of mass annual elephant migrations over several hundred kilometres (Roberts 1951, Dorst and Dandelot 1970, Sikes 1971).

It also does not fit in with the compression hypothesis as reported in many other African elephant sanctuaries (Buechner, Buss, Longhurst and Brooks 1963, Buss and Savidge 1966, Van Wyk and Fairall 1969, Anderson and Walker 1974, Williamson 1975, Eltringham 1977, Fairall 1979, Barnes and Douglas-Hamilton 1982, Pellew 1983). The compression theory implies a mass shift of elephant populations as a result of human pressure. Caughley (1976), from his experience in the Luangwa Valley, Zambia, questions the compression theory as the highest dry-season concentration of elephants there occurred outside the park where humans were also present, albeit in low densities, a situation similar to that of the Kaokoveld. Caughley then concludes that compression may not be a logical necessity to explain changes in habitat and density, a conclusion confirmed by the observations in the present study. This discrepancy between home range fidelity on the one hand and mass annual migration or forced mass population shifts (compression into sanctuaries) is difficult to explain but it may well prove to be a function of elephant population density and the climatic regime they occupy. It is postulated that elephant dispersal is a gradual process, related to elephant density and interspecific food competition, in which over-large family groups have to range over increasingly larger areas to satisfy their food and water requirements. Thus the elephants gradually increase their knowledge of areas adjacent to their original home range. The subsequent splitting of these large family groups might then result in new range occupation by the sub-groups once the elephants have acquired a knowledge of resource distribution in the new areas. This prerequisite of a knowledge about resource distribution, especially in desert regions with widely scattered food and water resources, might explain the desert-dwelling elephants' reluctance to be forced into new areas. In higher rainfall areas where food and water are relatively abundant, knowledge about resource distribution might not be vital and thus the elephants can be forced to new ranges.

The centre of the elephants' long-term spatial strategy is the relatively small localized dry season ranges near permanent water supplies. Rainfall and river floods, and particularly the spatial and temporary distribution thereof, are probably the primary environmental determinants of elephant movements. This influence is indirect, acting as it were through its effect on the state of the vegetation, which in turn provides all the food for the elephants. Important components of the short-term spatial strategy are the apparent ability of elephants to sense local rain storms or river floods over considerable distances, and their readiness to move to the areas affected.

The elephants' strategy of habitat utilization is therefore based on fixed immutable dry season ranges from where they make irregular use of more distant areas where rain has fallen or floods have occurred. These movements are largely unpredictable in terms of timing and direction, being governed by short-term rainfall patterns, but are predictable in terms of overall location according to individual home ranges. Return movements are predictable with considerable reliability if the dry season ranges of individual elephants are known. This flexible system of movements and the ability to move long distances to and from a fixed home base enables the elephants to make use of resources that are available only temporarily while at the same time reducing their impact on the area on which they depend for dry season survival.

CONCLUSIONS

Throughout this study it was clear that the desert-dwelling elephants confined their movements to the desert region west of the 150 mm isohyet and that no migration to and from the Etosha National Park takes place. Where home ranges overlap the desert-dwelling elephants do make contact with each other but only in the south-east of the study area did they make infrequent contact with elephants from the transitional population. Using only their geographical distribution and the degree of contact with other elephants, these elephants can be clearly demarcated as a distinct population. This phenomenon of natural population segregation in elephants where the members of a population limit their movements to a definable geographic region is not unique to the present study, but have been observed in a number of regions in Africa (Watson and Bell 1969, Laws 1970, Croze 1972, Ross, Field and Harrington 1976, Eltringham 1977, Sherry 1978, De Villiers 1981, Moss and Poole 1983, Pellew 1983, Western and Lindsay 1984, Dunham 1986, Merz 1986). This natural population segregation also corresponds with the marked home range fidelity observed in elephants in this study, which in turn highlights the importance of an intimate knowledge of the natural resources in a region. This is especially important in a desert region with only a few widely scattered food and water resources. Knowledge of such resource distribution and the elephants' own high degree of mobility and ability to go without water for extended periods, are regarded as the key factors of the survival of these elephants in the desert.

Density, seasonal distribution, daily movements, movements from water, drinking frequencies and migration of the desert-dwelling population in relation to those of other elephant populations are a manifestation of the climatic regime they occupy and the availability of food and water in proximity to each other. In the absence of extensive physiological tests, these elephants revealed no marked adaptational differences from those of other elephant populations but they rather revealed a development of natural elephant abilities to such a degree where they seemed to be better equipped to desert conditions than most other large mammals.

CHAPTER 6

HABITAT UTILIZATION AND THE ECOLOGICAL SIGNIFICANCE OF THE DESERT-DWELLING ELEPHANTS IN THE NORTHERN NAMIB DESERT.

INTRODUCTION

After man himself, no other animal has had as great effect on its habitat as the African elephant. This is mainly due to the large size and longevity of the elephant (Laws 1970). Where elephants have occurred in large numbers, their effect on the habitat was devastating (Buechner and Dawkins 1961, Buss 1961, Brooks and Buss 1962, Lamprey, Glover, Turner and Bell 1967, Laws _et al._ 1975, Watson and Bell 1969, Laws 1970, Wing and Buss 1970, Field 1971, Caughley 1976, Barnes 1980 and 1983, Pellew 1983, Weyerhaeuser 1985). The presence of elephants in the northern Namib Desert with its supposedly fragile ecological balance, low animal and plant densities and few waterholes, has caused concern regarding the impact of these elephants on their environment.

Against this background, one of the objectives of this study was to obtain information regarding the ecological impact of these elephants on their environment, other animals and in particular on the desert vegetation. This information _inter alia_ would lead to an assesment of the concept of carrying capacity for elephants in the desert area.

In determining the ecological impact of the elephants, the departure point of the present study was to consider only the salient indicating factors vital to preserve both the habitat and animals concerned. For this purpose it was first attempted to establish which habitat type is most important to the elephants concerned in terms of their survival and utilization and, then, to determine the elephants' impact on this habitat type.

METHODS

Data were collected at two levels:

1. Recording of overall distribution and densities of elephants and plants in each habitat category by aerial and ground surveys.

2. Determination of habitat utilization by the elephants and their influence on various ecological parameters by using selected methods.

HABITAT PREFERENCE

The distribution and densities of the desert-dwelling elephants in the different habitat types were determined by monthly aerial and ground surveys as previously described (Chapter 4). To minimize subjectiveness the different vegetation and physiognomic areas were simplified into forage habitat types as described in Table 18.

The exact location of each elephant sighted was recorded and the occupied habitats were then classified according to the seven forage habitat type categories listed in Table 18. Data from aerial and ground surveys were pooled as there was no significant difference between the seasonal frequency of different habitats occupied by the elephants between the two survey methods employed ($t = 1,86$; $p>0,05$; df=6). The observed locations of the elephants were plotted on a 1:250 000 map overlayed by a grid of 1 km^2 units.

To evaluate the elephants' habitat preference, the frequency and relative density of the elephants in each forage habitat were calculated on a seasonal and yearly basis. A preference index (P.I.) was calculated for each forage habitat type by a formula adopted from Pepin (1986) and Hillman (1979) where the value obtained ranges from -1,0 to +1,0, indicating the least and most preferred areas respectively. A value of zero indicates a random association and a value of -1,0 indicates that the area was not utilized at all. Four variables were used in the calculations, namely:

n_x - the number of elephants in forage habitat 'x'.

N_t - total number of elephants observed.

a_x - area of forage habitat 'x'.

A_t - total area covered by the elephant distribution.

n_x/N_t is the proportion of elephants recorded in habitat 'x' and

a_x/A_t is the proportion of the total area covered by habitat 'x'.

Table 18: Size (km^2) and description of the forage habitat categories used in habitat preference determination of the desert-dwelling elephants in the northern Namib Desert, South West Africa, between 1980 and 1983.

HABITAT TYPE	SIZE	PERCENTAGE OF STUDY AREA	BROAD DESCRIPTION
Flood plains	70	0,5	Abundance of shrubs and annual grasses on alluvial plains where water accumulates during river floods.
River courses	395	2,7	Dry river courses which support large trees and shrubs with mainly annual grasses.
Sandy plains	355	2,4	Wide deep sandy plains with mostly a perennial grass cover.
Rocky plains	3187	21,6	Shrubs and annual grasses on plains covered with rocks up to 300 mm in diameter.
Gravel plains	4715	32,0	Annual grasses and herbs on flat gravel plains with no trees or shrubs.
Mountains	5153	34,9	Extremely rocky disposition with mostly shrubs and annual grasses on steep slopes.
Sand dunes	875	5,9	High semi-permanent dunes with occasional annual grasses on the windward slopes.
Total	14750	100,0	

If $n_x/N_t > a_x/A_t$, then $\text{P.I.}(x) = \dfrac{1}{1 - a_x/A_t} \times (n_x/N_t - a_x/A_t)$

If $n_x/N_t < a_x/A_t$, then $\text{P.I.}(x) = \dfrac{1}{a_x/A_t} \times (n_x/N_t - a_x/A_t)$.

VEGETATION UTILIZATION

The objectives of this section were to determine elephant utilization of and possible damage to the vegetation in the different forage habitat types within the northern Namib Desert in relation to elephant densities and seasonal use. To determine elephant utilization of and damage to the vegetation, a series of transects were located throughout the major forage habitat types, in such a way as to cover the range of variation in terms of vegetation composition and previously observed habitat preferences. Transects were laid out in a north-south direction, except in river courses where the transects were laid out at right angles to i.e. across the width of the riverbeds. The transects in the river courses were 250 m long and the width was determined by the width of the riverine vegetation. Outside rivers the transects were 20 m wide and the length was determined by the area required to include at least 10 individuals of each dominant woody plant species. The number of woody plants in each transect was projected to plants per hectare to determine the density of woody plants in each forage habitat type (Anderson and Walker 1974).

Transect location in the forage habitat types outside river courses was determined randomly by dividing each habitat type into a series of squares and allocating a number to each square in order to use the table of random numbers. Alternative locations were selected where the first random location proved to be physically inaccessible. River courses were sampled through a series of transects over the length of a specific river. The results were compared in terms of differences in utilization and plant composition per habitat type.

Transects were limited to those forage habitat types representing permanent vegetation, e.g. trees and shrubs, as annual grasses and herbs were not constantly available for analysis in this arid region with its highly variable rainfall. Also, while annual grasses and herbs may be indicators of trend in higher rainfall regions, it was felt that the ephemeral nature of these plants in the northern Namib Desert would be little influenced by grazing and would give little information on animal use-related vegetation trends. Thus, forage habitat types such as the sand dunes, gravel plains, flood plains and sandy plains were not monitored to determine vegetation utilization and trends.

In those forage habitat types with permanent woody vegetation e.g. river courses, mountains and rocky plains, plants were rated according to elephant utilization or damage classes, adopted from Anderson and Walker (1974). The categories were limited in order to minimize subjectiveness namely:

Class 1 - no utilization.

Class 2 - slight utilization (1-25 per cent of canopy removed).

Class 3 - moderate utilization (26-75 per cent of canopy removed).

Class 4 - heavy utilization (76-90 per cent of canopy removed).

Class 5 - dead (91-100 per cent of canopy removed or uprooted).

A sixth class of plants killed by causes other than elephants was also used in the calculations. For comparative purposes utilization monitoring was also done in selected sites within the eastern elephant population's distribution range.

No attempt was made to distinguish between old and new elephant utilization because this proved to be too subjective in the arid climate. For example, it was found that utilization scars one month old could not be distinguished readily from scars six months old. Also, the low frequency in which some habitat types were utilized would lead to unreliable conclusions due to small sample sizes if only fresh utilization scars were taken into account. Thus, all elephant utilization, where no regrowth had yet occurred, between 1980 and 1983 were taken into account. The number of dead plants reported in this study, represent at least five years of elephant utilization as revealed by test transects in areas where the last known elephant utilization was in 1977. Dead plants from the latter areas could not be objectively distinguished from dead plants in other areas which were dead for less than two years as plant matter decomposition in the arid climate appeared to be extremely slow.

PREFERRED FOOD PLANTS

The primary objective was to distinguish preferred woody plant species from non-preferred ones in relation to elephant utilization, habitat type and species composition. In the context of this study, a 'preferred food species' is here defined as one which is utilized proportionally more frequently by elephants than its abundance in the available environment (Petrides 1975). For this purpose a preference ratio was calculated for each species, i.e. the percentage of a species utilized / percentage availability of that species. A species which is utilized in the same proportion as the proportion of that species on offer, has a preference ratio of one. Species having preference ratio values greater than one are preferred by elephants to those having preference ratio values of less than one. Species which are totally avoided, have a zero preference ratio (Barnes 1976, Ishwaran 1983).

Woody plant species in each forage habitat type were monitored and classified into elephant utilization classes as described under 'vegetation utilization'. Because a bias towards slightly utilized plants would be introduced if all utilized plants, regardless of the degree of utilization, were used in the calculations, weighting factors were incorporated (Barnes 1976). By means of these weighting factors estimates of the degree of elephant utilization were converted to the number of fully utilized plants (100 per cent of the canopy utilized) per species. The corresponding weighting coefficients for obtaining the number of fully utilized plants, were 0,25 for class 2; 0,75 for class 3; 0,9 for class 4 and 1,0 for class 5 according to the estimated percentage of canopy removed for each species.

Preference ratios were then calculated by using the following formula, as adapted from Petrides (1975) and Ishwaran (1983):

$$\text{Preference ratio (PR)} = \frac{\text{Percentage utilization (U)}}{\text{Percentage availability (A)}}$$

where

$$\text{Percentage utilization (U)} = 100 \times \frac{\text{Number of fully utilized woody plants in a species per unit area}}{\text{Total number of fully utilized woody plants in all species within the same area}}$$

and

$$\text{Percentage availability(A)} = 100 \times \frac{\text{Number of available woody plants in a species per unit area}}{\text{Total number of available woody plants in all species within the same area}}$$

BARK UTILIZATION

Because ring-barking seemed to be the major cause of elephant-induced tree mortality, bark utilization was monitored separately. Through a series of transects, a record was made of the percentage of tree girth at breast height from which bark had been removed from each large tree taller than 4 m (Thomson 1975, Barnes 1980, Short 1981). As in Caughley's (1976) study, no attempt was made to assess the rate of bark utilization or death by ring-barking because of the difficulty of establishing the date of death or utilization scars.

VEGETATION TRENDS

Aerial photographic monitoring

A technique, similar to the one developed by Croze (1974b), was used to measure changes in the numbers of large trees. Using three complete sets of aerial photographs, which covered a period of 20 years, 28 random plots along the Hoanib River bed were chosen (a transect ± every 2,0 km). On the 1963 set of photographs, convenient polygons encompassing the random points were demarked, using conspicuous landmarks (large trees, rocks etc.) as corner points. These polygons, obviously congruent on the sets of 1963, 1975 and 1983 photographs, were the sample plots and averaged 6,75 ±2,1 hectares on the ground. Under a mirror stereoscope each tree that stood out (higher than the shrub stratum of 2-3 m high) in each sample plot on the 1963 photographs was counted and compared with it's image in the photographs for 1975 and 1983.

On-the-spot examination of the aerial photographs, revealed that trees that stood out under the mirror stereoscope were taller than 4,0 m. As a result, all <u>Acacia albida</u>, <u>Acacia erioloba</u> and <u>Acacia tortilis</u> trees taller than 4,0 m were actually being counted. A few Colophospermum mopane and Combretum imberbe trees which occurred in this height class, were also sampled. Each tree was checked in consecutive photographs and annotated when missing. It was found that 'new' trees which apparently had grown into the >4,0 m height class since 1963 were counted additionally in 1975 and 1983. The method used therefore also yields a large tree recruitment rate. The percentage canopy cover for all plants per plot (trees and shrubs) was also estimated for the 1963 and 1975 sample plots. However, the presence of long shadows in the 1983 photographs made it difficult to distinguish between individual shrubs' canopies. This would have resulted in an overestimation of canopy cover and were thus excluded from the results.

Age structure and mortality of selected tree species

Tree species were enumerated in transects as already described. The relative age structure of selected trees was determined by measuring the trunk girth above the basal swelling rather than measuring the girth at breast height, because of the tendency of trunks to fork below breast height. Tree height was not used for estimating relative age structure because of the difficulty in measuring large trees accurately. However, height was used to determine the number of established seedlings (plants ≤1,5>0,5 m tall) and established young trees (plants ≤4>1,5 m tall) against mature trees (>4 m) that reproduce seeds. Acacia albida trees in the Hoanib River were again used as indicators of trends, mainly because the Hoanib River had the highest concentration of elephants during the hot dry season, but also because Acacia albida was the only single-stemmed tree species which occurred in relatively large numbers in the Hoanib Riverbed. Acacia erioloba occurred in relatively low numbers and other large tree species like Colophospermum mopane and Combretum imberbe tended to form multi-stemmed thickets which were impossible to measure for relative age structure. Tree mortality was determined by counting the number of dead trees in each transect and by recording the cause of death.

RESULTS

HABITAT PREFERENCE

By comparing the frequency distribution of the number of 1 km^2 units containing 0,1,2,3....n elephants with the Poisson distribution, the distribution of elephants in the northern Namib Desert was found to be non-random ($\chi^2 = 5148,22$; $p<0,001$; df=3). The departure from randomness was due to an over-representation of units containing two or more locations. The distribution of the elephants was obviously also not uniform but showed a clumped distribution pattern, indicating a preponderance for certain habitat types ($\chi^2 = 22114,7$; $p<0,001$; df=6).

Operationally, the best available elephant forage habitat in the northern Namib Desert is defined as that with which the elephants associated most. That is, that forage habitat in which the elephants spent most of their time, occur in the highest density and show the highest preference in relation to the elephants' overall distribution and sizes of the forage habitats. Table 19 shows the percentage frequency, relative density and preference index of the elephants in each forage habitat type for the data summarized over the period 1980 to 1983. The percentage frequency of elephants observed in each forage habitat is also regarded as an indication of time spent in each forage habitat type.

Inspection of the data in Table 19 reveals that the elephants spent most of their time in the river course forage habitat type and that they showed the highest preference index for this type. However, flood plains had the highest relative density of elephants although the elephants spent less time in the flood plains than in the river courses. All other forage habitat types had a negative preference index, with gravel plains being the forage habitat type with which the elephants least associated with and sandy plains being the habitat in which the elephants spend the least amount of time. Mountains and rocky plains forage habitats were the only other forage habitats in which the elephants spent any amount of time but as a result of the huge sizes of these habitats, the calculations indicate a low preference index by elephants for them.

It is clear that river course forage habitats were the most utilized elephant habitat in the northern Namib Desert. This, however, does not mean that the river course forage habitat is the most preferred habitat, but that it probably is a function of

Table 19: Habitat utilization by the desert-dwelling elephants in the northern Namib Desert, South West Africa, depicting habitat-specific relative densities (elephants/km^2), percentage frequencies of elephant occurrence in and preference indexes of the elephants for the seven forage habitat types during the period 1980 to 1983.

HABITAT TYPE	PERCENTAGE FREQUENCY OF ELEPHANTS IN HABITAT	RELATIVE DENSITY OF ELEPHANTS IN HABITAT	PREFERENCE INDEX OF ELEPHANTS FOR HABITAT
River courses	53,07	1,75	0,52
Flood plains	18,71	3,49	0,18
Mountains	12,81	0,03	-0,63
Rocky plains	7,75	0,03	-0,64
Sand dunes	3,22	0,05	-0,46
Gravel plains	2,84	0,01	-0,91
Sandy plains	1,61	0,07	-0,24

preference and availability. The most preferred or ideal forage habitat might well have been the flood plains (indicated by the high relative density of elephants there), but it is only available during the wet season. This restricted availability also explains the low percentage frequency (time spent) in which the elephants were observed in the flood plains. This point is further illustrated in Table 20 where the seasonal habitat utilization data indicate that the elephants show a marked preponderance for the flood plains during the wet season almost to the exclusion of the other habitat types at that time. However, as the dry season commenced, the availability of green grass and shrubs on the flood plains deteriorate rapidly, with the the result that the elephants shift their utilization to the river course forage habitat and to a limited extent also to some of the other habitat types.

Figure 47 shows the changes in elephant forage habitat preferences on a seasonal basis for each study year. As previously mentioned, there was an overall tendency for elephants to avoid other forage habitats during the wet season with a high preference for the flood plains. However, the utilization of the flood plains was dependent on the rainfall and river floods and fluctuated accordingly. The only forage habitat which showed a steady positive preference, little influenced by rainfall, was the river course forage habitat. To a lesser degree this was also evident in the mountain and rocky plains forage habitats, although the latter habitats showed a low preference index. The gravel plains had the lowest preference index, remaining low

Table 20: Seasonal habitat utilization by the desert-dwelling elephants in the northern Namib Desert, South West Africa, between 1981 and 1983.

HABITAT TYPE	SEASON						DEVIATION FROM A 1:1:1 RATIO	
	Wet		Cold dry		Hot dry		Chi-square	P-value
	n	%	n	%	n	%	value	(df =2)
Flood plains	110	60,44	42	13,08	92	11,49	52,96	<0,001
River courses	49	26,93	144	44,86	499	62,29	13,99	<0,001
Sandy plains	0	0,00	0	0,00	21	2,62	5,26	<0,05
Rocky plains	0	0,00	40	12,47	61	7,62	11,79	<0,005
Mountains	13	7,14	66	20,56	88	10,99	7,41	<0,05
Gravel plains	0	0,00	14	4,36	23	2,87	4,08	>0,05
Sand dunes	10	5,49	15	4,67	17	2,12	1,51	>0,05
Total	182	100,00	321	100,00	801	100,00	-	-

n = number of elephants observed in a given habitat.

% = percentage of all elephants observed during a specific season in a given habitat.

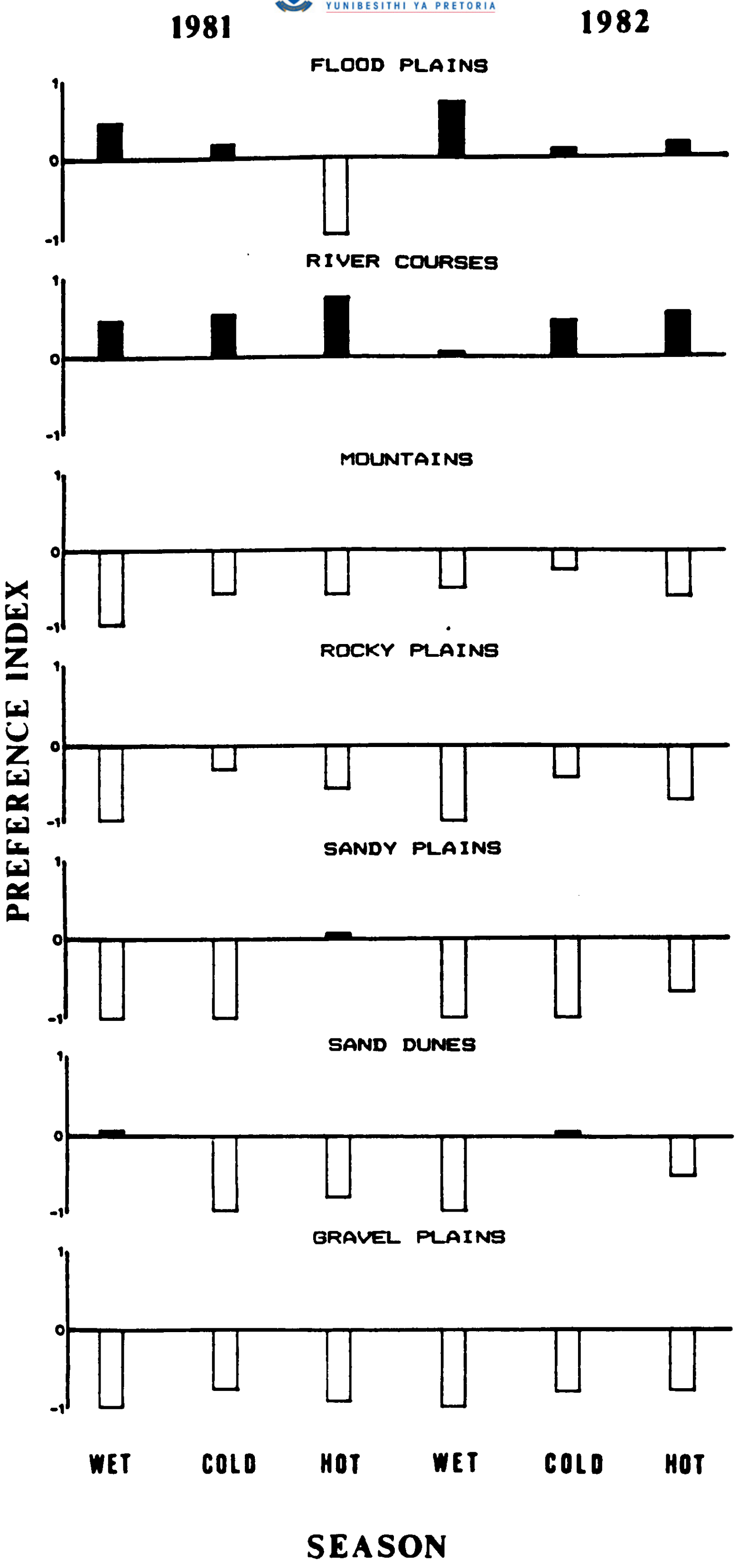


Figure 47: Seasonal changes in habitat preference of the desert-dwelling elephants for seven different forage habitat types in the northern Namib Desert region of the Kaokoveld, South West Africa. Where +1 indicates an absolute positive association and -1 an absolute avoidance.

throughout the seasons, indicating that this habitat is mostly avoided by the elephants.

VEGETATION UTILIZATION

In the three forage habitat types monitored for this aspect in the northern Namib Desert, a total of 2167 woody plants in 39 transects were examined for utilization by the desert-dwelling elephants. Seventy-one per cent of the woody plants examined were not utilized or damaged in any way by the elephants. Of the woody plants utilized (29 per cent), 16 per cent were only slightly utilized, 10 per cent were moderately utilized and 2 per cent were utilized heavily but were not dead. Although a total of 8 per cent of the woody plants sampled were dead, only 1 per cent of all the plants sampled, had been killed by elephants and the rest by floods, drought or fire.

Table 21 summarises information on woody plant composition of and utilization by elephants in the different forage habitat types. The river courses, mountains and rocky plains forage habitat types represent utilization by the desert-dwelling elephants, while the eastern savanna represents utilization by the eastern elephant population. Caution must be exercised in interpreting the data on woody plant densities as it cannot be regarded as an indication of plant biomass. For example, although the river course forage habitat has the lowest density of woody plants, the mean height of woody plants in this habitat type is 3,13 ±3,15 m (n = 1293) compared to that of the mountain habitat type

Table 21: Summary of woody plant composition, elephant utilization and elephant induced mortality of woody plants in four different forage habitat types between 1980 and 1983 within the Kaokoveld, South West Africa.

FORAGE HABITAT TYPE	NUMBER OF WOODY PLANT SPECIES	DENSITY OF WOODY PLANTS PER HECTARE	PERCENTAGE WOODY PLANTS NOT UTILIZED	PERCENTAGE WOODY PLANTS UTILIZED	PERCENTAGE WOODY PLANTS KILLED
River courses	17	33,32	55,14	44,86	1,93
Mountains	19	198,55	94,14	5,86	1,09
Rocky plains	18	172,63	89,01	11,89	0,61
Eastern Savanna	7	321,00	9,19	90,81	1,74

* Only woody plant species (trees and shrubs) occurring at a density of more than 0,1 plants per hectare were used in the calculations.

where the a mean height is 0,72 ±0,74 m (n = 546), the rocky plains with 0,92 ± 0,78 m (n = 328) and the eastern savanna with 2,09 ±1,16 m (n= 805).

There was a signifantly larger proportion of woody plants utilized by elephants in the eastern savanna forage habitat than in any of the three forage habitat types representing the northern Namib Desert (χ^2= 167,42 to 386,12; $p<0,001$; df=1). In the northern Namib Desert, the incidence of woody plants utilized by elephants was significantly higher in the river course forage habitat than in the habitat types outside river courses e.g. mountains and rocky plains (χ^2= 59,27 and 151,26; $p<0,001$; df=1). However, the proportion of woody plants utilized in the mountain and rocky plains habitat types respectively was not significantly different (χ^2= 2,84; $p>0,05$; df=1).

Figure 48 compares the utilization of woody plants in the forage habitat types utilized by the desert-dwelling elephants and a forage habitat type utilized by the eastern elephant population in the Kaokoveld. As no significant differences could be detected between the proportion of woody plants utilized in the mountains and rocky plains forage habitat types, these two forage habitat types were pooled as a forage habitat representing the vegetation occurring outside the river courses. Examination of Figure 48 illustrates the differences in the percentage of woody plants utilized by elephants in the various forage habitat types. Whereas most available woody plants were utilized in eastern

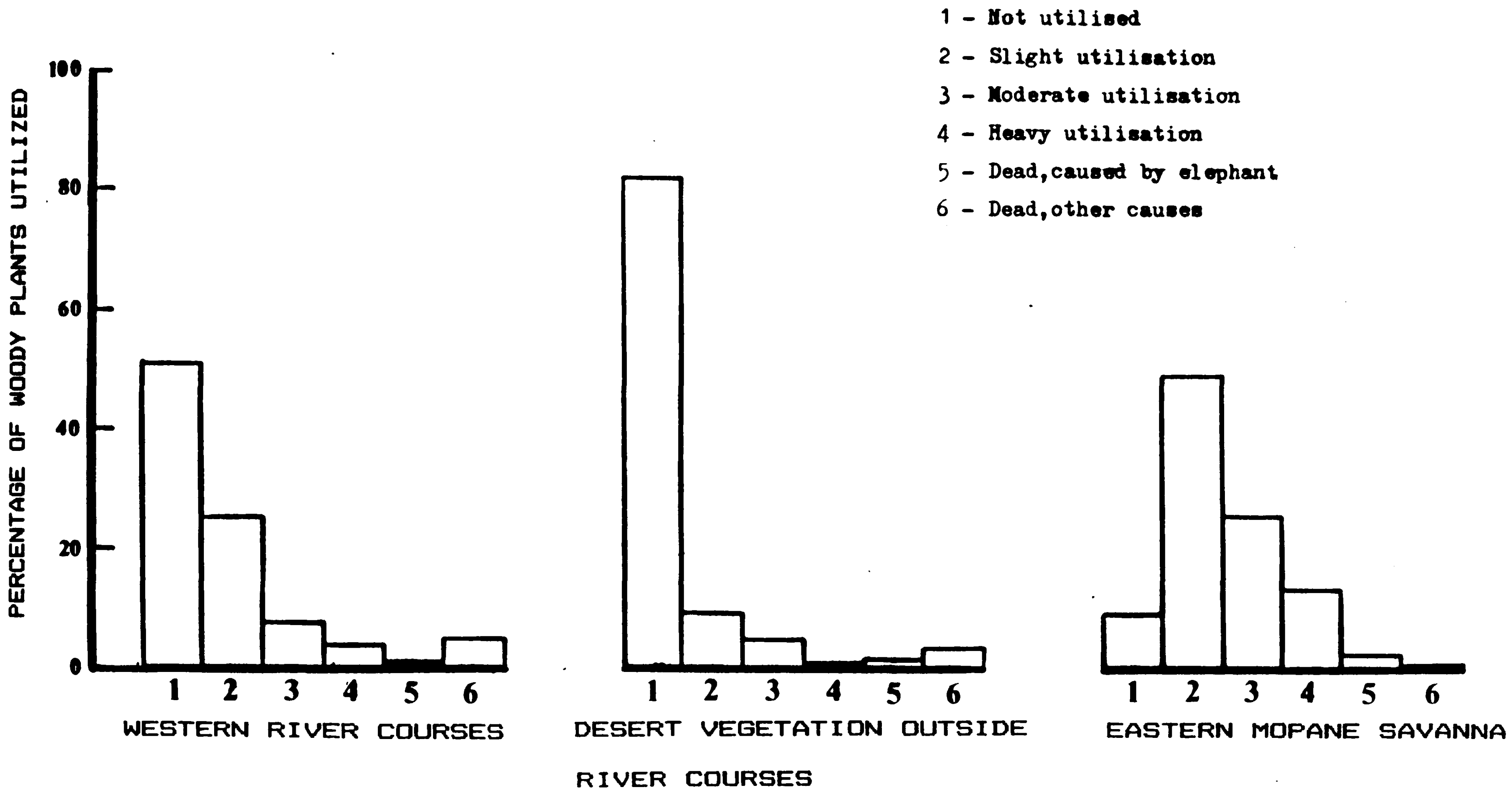


Figure 48: Elephant utilization of woody plants in the Kaokoveld, South West Africa, between 1980 and 1983, shown as a comparison between different forage habitat types within the elephant's distribution range.

Kaokoveld, less than half the available woody plants were utilized by elephants in the river course forage habitats of the northern Namib Desert and less than 9 per cent of the available woody plants were utilized in the habitat types outside the river courses. From Figure 48 it can also be seen that a higher proportion of woody plants (5 per cent of the woody plants) in river course forage habitats was killed by causes other than elephants. This was due to trees in the dry river beds being undermined by flood waters and also being destroyed by occasional fires, caused by the local people to improve winter grazing.

The incidence of woody plants which were slightly or moderately utilized by elephants (elephant utilization classes two and three) was similar in all four forage habitat types ($\chi^2=1{,}01$; $p>0{,}05$; df=2). However, a significantly higher proportion of woody plants was heavily utilized or damaged (76-90 per cent of the canopy removed) by the eastern elephant population ($\chi^2=14{,}93$; $p<0{,}05$; df=2). In contrast again, of the woody plants utilized, a significantly larger proportion was killed by elephants in forage habitat types outside river courses ($\chi^2=20{,}01$; $p<0{,}001$; df=2) This was due to the small sizes of woody plants in the mountains and rocky plains forage habitat types, which were often pulled out of the ground entirely by elephants when feeding. However, of the woody plants utilized in the northern Namib Desert, the number that were heavily utilized or killed by elephants were insignificant ($\chi^2=364{,}88$; $p<0{,}001$; df=1). Also, of all the dead woody plants, a significant majority were killed by causes other than elephants ($\chi^2=20{,}45$; $p<0{,}001$; df=1).

PREFERRED FOOD PLANTS

A total of 33 woody plant species which occurred at densities of more than 0,1 plants per hectare each were recorded in 39 transects during the present study in the northern Namib Desert. Tables 22 to 24 show the density, mean height, percentage availability, percentage of plants fully utilized and preference ratios shown by the elephants for the various woody plant species in the river courses, mountains and rocky plains forage habitat types respectively. Direct comparison between the three habitat types was impossible as only three woody plants species occurred abundantly in all three habitat types, namely <u>Colophospermum mopane</u>, <u>Boscia foetida</u> and <u>Maerua schinzii</u>. There was no significant difference in the preference ratio values of these latter three species as shown by elephants in the three different forage habitat types ($t = 0{,}09$ to $1{,}84$; $p > 0{,}05$; $df=4$).

Paired t-tests between the ten preferred species which occurred in both the mountain and rocky plain forage habitat types (Tables 23 and 24) showed no significant differences in preference ratio values or percentage availability of these species in the different habitat types ($t=1{,}127$ and $t=-0{,}248$; $p>0{,}05$; $df=18$).

Examination of all preferred species in all three habitat types revealed no linear relationship between the preference ratio values and percentage availability($r=-0{,}366$; $t=-1{,}924$; $p>0{,}05$;

Table 22: Elephant feeding preference ratios for woody plant species in the river course forage habitat type in the northern Namib Desert, South West Africa, between 1980 and 1983.

WOODY PLANT SPECIES	DENSITY: PLANTS PER HECTARE	PLANT HEIGHT IN METRES		PERCENTAGE PLANT AVAILABILITY	PERCENTAGE FULLY UTILIZED PLANTS	PREFERENCE RATIO*
		Mean	SD			
Cordia gharaf	0,26	2,02	±0,61	0,77	2,21	2,87
Combretum wattii	0,10	1,03	±0,78	0,31	0,78	2,52
Colophospermum mopane	6,85	4,02	±2,17	20,73	40,88	1,97
Tamarix usneoides	1,55	3,29	±0,99	4,64	9,09	1,95
Boscia foetida	1,31	1,84	±1,43	3,94	7,36	1,87
Combretum imberbe	1,52	4,24	±4,25	4,56	8,26	1,81
Maerua schinzii	0,28	3,61	±2,15	1,08	1,58	1,46
Balanites welwitschii	1,80	3,02	±1,25	5,41	6,03	1,11
Salvadora persica	3,09	2,52	±1,33	9,59	6,54	0,68
Acacia erioloba	2,81	5,83	±3,94	8,28	5,25	0,61
Acacia albida	3,68	5,62	±5,32	11,83	6,68	0,56
Pechuel-Loeschea leubnitziae	2,22	1,08	±0,18	6,65	3,14	0,47
Euclea pseudebenus	0,46	2,63	±1,04	1,39	0,17	0,12
Salsola spp.	5,31	0,62	±0,21	15,93	1,95	0,12
Acacia tortilis	0,26	7,67	±4,03	0,77	0,08	0,10
Mundulea sericea	0,33	0,82	±0,06	1,01	0,00	0,00
Suaeda plumosa	1,03	0,58	±0,19	3,09	0,00	0,00

$$* \text{ Preference ratio} = \frac{\text{Percentage of fully utilized plants}}{\text{Percentage plant availability}}$$

Table 23: Elephant feeding preference ratios for woody plant species in the mountain forage habitat type in the northern Namib Desert, South West Africa, between 1980 and 1983.

WOODY PLANT SPECIES	DENSITY: PLANTS PER HECTARE	PLANT HEIGHT IN METRES		PERCENTAGE PLANT AVAILABILITY	PERCENTAGE OF FULLY UTILIZED PLANTS	PREFERENCE RATIO*
		Mean	SD			
Colophospermum mopane	0,36	1,00	±0,00	0,18	3,86	21,44
Pachypodium lealii	1,09	1,57	±0,81	0,55	8,99	16,35
Sesamothamnus spp.	0,36	1,00	±0,00	0,18	1,29	7,17
Terminalia prunioides	4,73	1,70	±0,28	2,38	12,34	5,18
Boscia foetida	8,00	1,18	±0,81	4,03	12,85	3,19
Parkinsonia africana	1,82	2.50	±1,41	0,92	2,57	2,79
Adenolobus spp.	2,91	0,13	±0,06	1,47	3,86	2,63
Commiphora kraeuseliana	19,27	0,92	±0,24	9,71	24,68	2,54
Commiphora multijuga	1,09	1,50	±0,50	0,55	1,29	2,35
Maerua schinzii	2,91	2,63	±1,06	1,47	2,57	1,75
Commiphora virgata	22,55	0,82	±0,26	11,36	17,99	1,58
Commiphora wildii	9,82	0,52	±0,21	5,49	5,14	0,94
Commiphora saxicola	27,27	0,61	±0,63	13,74	2,57	0,19
Euphorbia damarana	10,55	1,64	±0,51	5,31	0,00	0,00
Calicorema capitata	3,27	0,40	±0,18	1,65	0,00	0,00
Petalidium spp.	81,82	0,38	±0,19	41,21	0,00	0,00
Salvadora persica	0,36	0,50	±0,00	0,18	0,00	0,00
Catophractes alexandri	0,36	0,50	±0,00	0,18	0,00	0,00

$$*\text{Preference ratio} = \frac{\text{Percentage fully utilized plants}}{\text{Percentage plant availability}}$$

Table 24: Elephant feeding preference ratios for woody plant species in the rocky plain forage habitat type in the northern Namib Desert, South West Africa, between 1980 and 1983.

WOODY PLANT SPECIES	DENSITY: PLANTS PER HECTARE	PLANT HEIGHT IN METRES Mean	PLANT HEIGHT IN METRES SD	PERCENTAGE PLANT AVAILABILITY	PERCENTAGE OF FULLY UTILIZED PLANTS	PREFERENCE RATIO*
Pachypodium lealii	0,53	1,50	±0,00	0,30	3,99	13,33
Parkinsonia africana	1,58	3,50	±0,71	0,91	6,12	6,73
Colophospermum mopane	8,42	1,41	±0,71	4,88	26,59	5,45
Terminalia prunioides	16,84	1,69	±0,64	9,76	28,72	2,94
Boscia foetida	5,26	0,72	±0,31	3,05	7,98	2,62
Adenolobus spp.	13,68	0,38	±0,46	7,93	13,29	1,66
Commiphora kraeuseliana	10,00	0,62	±0,19	5,79	9,31	1,61
Maerua schinzii	3,68	2,10	±0,55	2,13	0,00	0,00
Commiphora virgata	2,63	0,98	±0,29	1,52	0,00	0,00
Commiphora wildii	1,22	0,40	±0,00	0,30	0,00	0,00
Commiphora saxicola	3,68	0,97	±0,35	2,13	0,00	0,00
Euphorbia damarana	8,95	1,86	±0,55	5,18	0,00	0,00
Calicorema capitata	3,16	0,41	±0,07	1,83	0,00	0,00
Petalidium spp.	77,89	0,39	±0,07	45,12	0,00	0,00
Catophractes alexandri	13,16	1,15	±0,09	7,62	0,00	0,00
Sesamothamnus spp.	0,53	1,00	±0,00	0,30	0,00	0,00
Asparagus africana	0,53	0,80	±0,00	0,30	0,00	0,00

$$* \text{ Preference ratio} = \frac{\text{Percentage of fully utilized plants}}{\text{Percentage plant availability}}$$

df=25). Similarly, there was no significant linear relationship between mean species height and preference ratio values (r=-0,025; t=-0,179; p>0,05; df=50).

Incorporating data from all three forage habitat types representing woody plant species in the northern Namib Desert, a preference order for the most preferred woody food plants of the desert-dwelling elephants was constructed. Table 25 lists the woody plant species in the northern Namib Desert with a preference ratio value of more than one in order of preference. Cordia gharaf, Pachypodium lealii and Combretum wattii are clearly the most preferred food plants of the desert-dwelling elephants. However, these latter plants all occur at a low density with a low percentage availability and thus contribute little to the diet of the elephants in terms of bulk and can only be considered choice food morsels. The most important food plants in the diet of the desert-dwelling elephants might well be Colophospermum mopane, Tamarix usneoides and Combretum imberbe, all of which have a high preference ratio value coupled to a relatively high density and percentage availability. Again actual plant biomass was not taken into consideration and the plant species listed above might not be the most important food species in terms of bulk.

The woody plants listed in Table 25 which occur at densities of more than one plant per hectare, can be considered as the most important woody plants in the diet of the desert-dwelling elephants as far as bulk is concerned. However, in separate

Table 25: Woody plant species preferred as food plants by the desert-dwelling elephants in the northern Namib Desert, South West Africa between 1980 and 1983. Incorporating data from the three forage habitat types representing woody plants.

WOODY PLANT SPECIES	PREFERENCE RATIO*	PERCENTAGE PLANT AVAILABILITY	PERCENTAGE OF FULLY UTILIZED PLANTS	DENSITY: PLANTS PER HECTARE
Cordia gharaf	4,26	0,46	1,96	0,23
Pachypodium lealii	4,17	0,18	0,75	0,09
Combretum wattii	3,83	0,18	0,69	0,09
Tamarix usneoides	2,91	2,77	8,07	1,38
Colophospermum mopane	2,89	13,15	38,02	6,56
Combretum imberbe	2,69	2,72	7,33	1,36
Boscia foetida	1,88	3,83	7,21	1,91
Balanites welwitschii	1,66	3,23	5,35	1,61
Parkinsonia africana	1,32	0,37	0,49	0,18
Maerua schinzii	1,16	1,34	1,55	0,67
Terminalia prunioides	1,13	2,08	2,35	1,04
Commiphora spp.	1,09	0,55	0,60	0,28
Salvadora persica	1,01	5,77	5,81	2,88

$$* \text{ Preference ratio} = \frac{\text{Percentage of fully utilized plants}}{\text{Percentage plant availability}}$$

records of direct observations on feeding elephants, virtually all plants (with the exception of the poisonous Euphorbia species) that occur in the northern Namib Desert were at some stage taken by elephants albeit infrequently so. This does not necessarily mean that all these plants were being utilized as food plants. For example, on two occasions it was witnessed that the elephants spit out chewed Euclea pseudebenus leaves over their ears and heads, presumably as a means of cooling off. Also, the fibrous parts of chewed Welwitschia mirabilis leaves, which were presumably being utilized for their moisture content only, were often spat out.

BARK UTILIZATION

Bark utilization was not included in the classification of woody plants into elephant utilization classes because the respective utilization classes referred to the percentage of canopy removed. Also, it was impossible to establish the age of bark scars reliably within a reasonable time span. Most bark utilization scars appeared to be very old as was verified by comparing photographs of Acacia albida trees, taken in 1975 with the same trees in 1982. On the available photographs (n=3), no differences in the amount or pattern of the scars could be distinguished. Fresh scars were observed on only four trees between 1980 and 1983. These observations suggested that bark stripping or utilization was not done on a regular basis by the desert-dwelling elephants, but that it probably occurred sporadically.

Nevertheless, because concern has been expressed elsewhere by other authors (e.g:-Schoeman 1982) regarding the impact of the elephants on the conspicuous trees in the river courses, these trees were the subject of a separate investigation into bark utilization (stripping) by the elephants concerned.

Throughout the northern Namib Desert, bark utilization scars were observed on only three tree species, namely _Acacia albida_, _Acacia erioloba_ and _Colophospermum mopane_. On _Colophospermum mopane_ trees, bark utilization scars occurred infrequently and only 1,4 per cent of all mopane trees checked (n=285) showed signs of bark utilization. Of all the mature (>4m tall) _Acacia albida_ trees checked (n=213) in the study area, 68 per cent had bark utilization scars and 2,3 per cent of these trees were killed through ring-barking by elephants. Of the mature _Acacia erioloba_ trees (n=91), 39 per cent had bark utilization scars and 1,6 per cent had been killed. A further 3,3 per cent of _Acacia albida_ trees and 1,6 per cent of _Acacia erioloba_ trees had more than 80 per cent of their bark utilized in relation to their trunk circumference at breast height. Although still alive, these trees are very vulnerable to further utilization and might soon die.

Table 26 is a summary of the percentage occurrence of bark utilization scars in mature _Acacia albida_ and _Acacia erioloba_ in the Hoanib and Hoarusib rivers. In the Huab river, the only other river within the elephant's distribution range with a large population of _Acacia albida_ and _Acacia erioloba_ trees, only 7 percent of the trees were affected. From Table 26 it can be seen

Table 26: Percentage occurrence of bark utilization scars by elephants in mature (>4 m) *Acacia albida* (n=194) and *Acacia erioloba* (n=61) trees in the larger river courses of the northern Namib Desert, South West Africa, during a survey conducted in 1982.

ITEM	HOANIB RIVER		HOARUSIB RIVER	
	Percentage of *Acacia albida* trees effected	Percentage of *Acacia erioloba* trees effected	Percentage of *Acacia albida* trees effected	Percentage of *Acacia eriolba* trees effected
Bark utilization categories*				
Not utilized	28,2	33,3	36,5	69,6
1-5 per cent	24,7	20,0	50,0	8,7
6-20 per cent	15,5	33,3	7,7	8,7
21-40 per cent	10,6	0,0	3,9	4,3
41-60 per cent	7,0	6,7	1,9	4,3
61-80 per cent	4,9	0,0	0,0	2,2
81-99 per cent	5,6	6,7	0,0	0,0
Ring-barked (100 per cent)	3,5	0,0	0,0	2,2

* Expressed as the percentage of bark utilized by elephants in relation to the tree trunk circumference at breast height.

that the largest proportion of bark utilization occurred in the Hoanib river, reflecting the density of elephants in this river (Chapter 3). The combined data from both rivers show that although the largest proportion (70 per cent) of *Acacia albida* trees had scars of bark utilization, most of the *Acacia albida* trees utilized (75 per cent) had less than 20 per cent of their bark utilized in relation to their trunk circumference. In *Acacia erioloba* trees, 39 per cent of the trees sampled were effected and 90 per cent of the latter trees had less than 20 per cent of their bark utilized. Again it must be emphasized that the utilization scars recorded represent at least eight years of utilization and probably much longer since bark regrowth appear to be minimal.

Although occurring at a low frequency (Table 26), ring-barking was the main cause of elephant-induced mortality in mature (>4 m tall) *Acacia albida* trees as illustrated in Figure 49 where there is a significant linear relationship between bark utilization and tree mortality ($r=-0,92$; $t=5,14$; $p<0,01$; $df=5$). There was also a significant negative linear correlation between bark utilization and distance of the trees involved from open water in the Hoanib river ($r=-0,92$; $t=-4,73$; $p<0,01$; $df=5$). Up to 20 km away from water a relatively high proportion of mature trees was damaged by bark utilization (Fig. 49), after which a significantly small proportion of trees were affected ($\chi^2=19,01$; $p<0,001$; $df=1$). There was no linear correlation between trees killed by causes other than elephants and distance away from water ($r=0,11$; $t=0,22$; $p>0,05$; $df=5$). Neither was there any correlation between

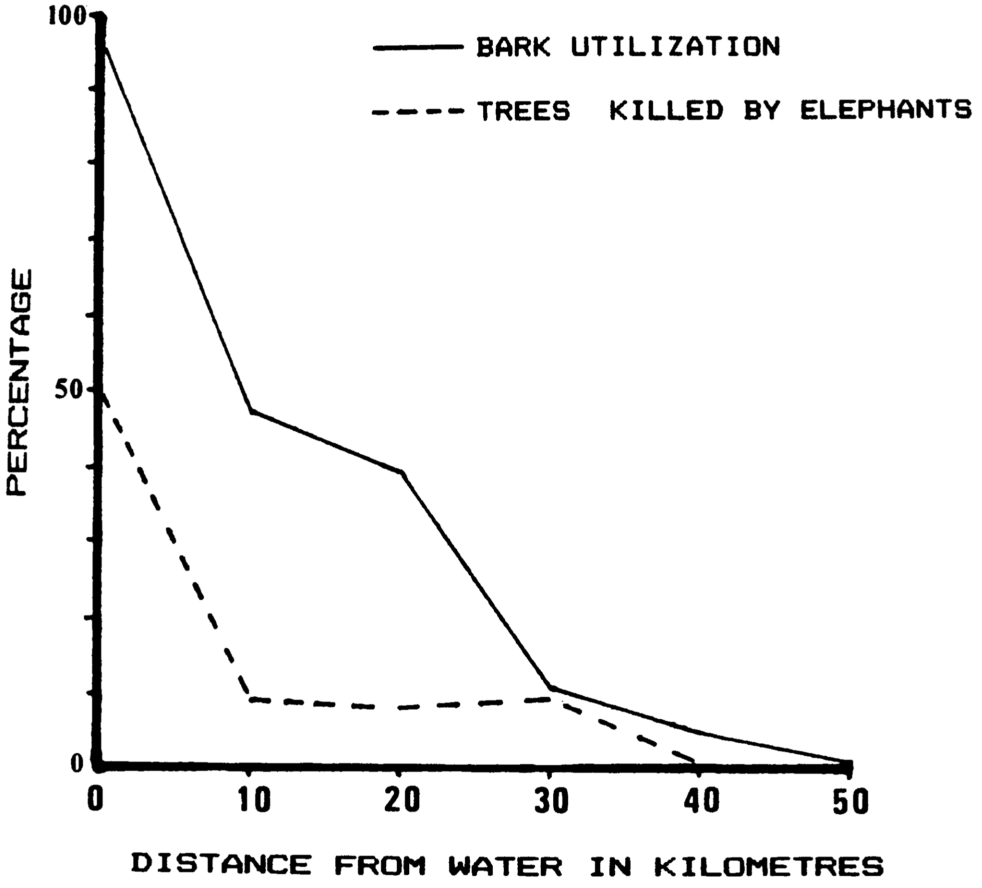


Figure 49: Percentage bark utilization of Acacia albida trees and percentage of Acacia albida trees killed by the desert-dwelling elephants in relation to distance from water in the Hoanib River, northern Namib Desert region of the Kaokoveld, South West Africa, during a survey done in 1982.

trees killed by elephants and tree density ($r=-0,52$; $t=-1,21$; $p>0,05$; df=1).

VEGETATION TRENDS

The aim of this investigation was to discover possible long-term trends in the vegetation of the northern Namib Desert, as related to past and present elephant utilization.

Aerial photographic monitoring

Table 27 is a summary of aerial photographic tree counts in the Hoanib River in 28 congruent sample plots during 1963, 1975 and 1983 respectively. As mentioned earlier, these numbers only represent trees taller than 4,0 m. There were no significant differences in the total number of tall trees counted during the three time periods ($F=0,006$; $p>0,05$; $df_1=2$, $df_2=83$). Similarly, between any two time periods, the numbers of tall trees counted were basically constant ($t=0,01$ to $0,09$; $p>0,05$; df=54).

The mean loss per plot in the Hoanib River over the 20-year period was 1,14 ±1,24 tall trees (>4m). This is equivalent to 32 trees over the whole 189 ha sampled in the survey, and represents a loss of 7 per cent over the 20-years period, or 0,4 per cent per year. From the data it can be calculated that in 1983 there was an estimated number of 2097 tall trees (>4,0 m tall) in the Hoanib River bed area (900 ha X 2,33 trees per ha). If the

Table 27: Changes in the number of large trees (> 4 m tall) counted in 28 congruent aerial photographic plots (6,75 ±2,1 ha in size) in three successive time periods in the western Hoanib River of the northern Namib Desert, South West Africa.

PARAMETERS INVOLVED	1963	1975	1983
Total number of trees	450	452	441
Mean number and SD of trees per plot	16,07±14,7	16,14±14,6	15,75±14,4
Number of trees per hectare	2,38	2,39	2,33
Percentage canopy cover of all plants	14,25	16,14	see text
Number of trees missing since previous period	-	11	21
Number of trees gained since previous period	-	13	10
Percentage change in number of trees since previous period	-	+0,44	-2,43

numbers of trees killed by elephants and other causes remained constant and if no replacement of trees by recruitment occurred, then all of the tall trees in the western Hoanib River will be gone in 285 years time. - a rather superfluous calculation. Also this calculation does not account for new recruitments to the tall tree class over the 20-year interval of the survey. The mean gain per plot over the 20-year period was 0,82 ±1,09 trees. This is equivalent to 23 trees, a rate of gain of 5 per cent over the 20 years, or 0,3 per cent per year. Therefore, the percentage change since 1963 (loss - gain) was 2 per cent over 20 years, or a rate of loss of 0,1 per cent per year. For all practical purposes this rate of loss is insignificant and the number of tall trees in the Hoanib River appear to be stable.

One must also bear in mind that the above results included all causes of death, many of which could not be attributed to elephants. At least 12 of the trees that were recorded missing in 1983 as opposed to 1975 had been undermined and washed away during the excessive floods of 1982 when the river broke through the dune belt to the sea, a phenomenon which had last occurred before 1963 (Karlowa pers. comm. 1982) with probably the same destruction to tall trees as in the 1982 floods. This might explain the apparent increase in the number of tall trees as sampled in 1975 when there had been no excessive floods in 12 years.

E. Karlowa, Private bag 5001, Swakopmund.

Age structure and mortality of *Acacia albida* trees

Figure 50 shows the relative age structure of all the *Acacia albida* plants sampled (n=206) in the Hoanib River which were still alive in 1982, in terms of trunk diameter classes. Seedlings less than 0,5 m tall, although abundant after the 1982 floods, mostly died the following year and were not included in the calculations. Dead trees were also not included in the age-structure calculations. All relative age stages were present and the structure shows a reverse J-shaped curve.

In terms of height classes, which were recorded separately, 25 per cent of all *Acacia albida* plants sampled (n=206) in the Hoanib River in 1982, were regarded as established seedlings which were more than two wet seasons old (plants ≤1,5>0,5 m tall). Another 22 per cent of *Acacia albida* plants were regarded as established young trees (trees ≤4>1,5 m tall) and the remaining 53 per cent were regarded as mature trees (>4 m tall). A total of 13 per cent of all the *Acacia albida* plants sampled (n=238) were dead. Six per cent of all *Acacia albida* plants sampled were judged to have been killed by elephants and 7 per cent by other causes. As mentioned earlier, rate of death could not be established, and the data above represent at least eight years of elephant utilization.

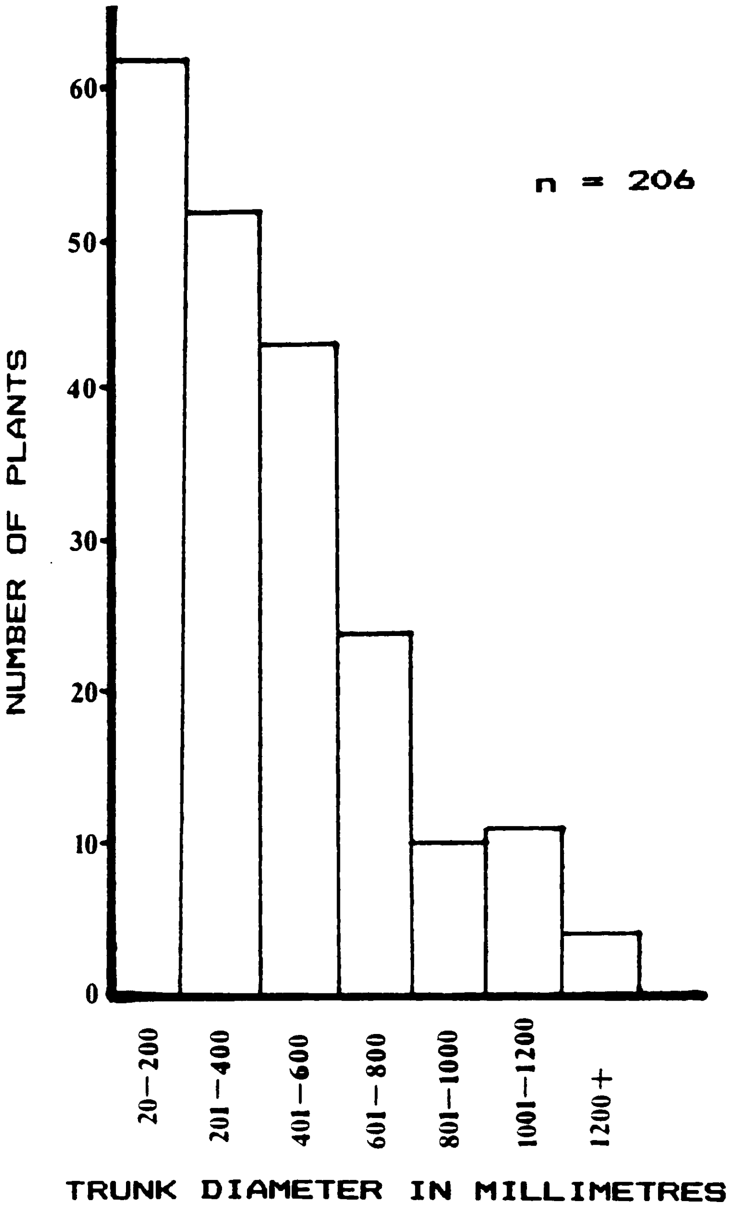


Figure 50: Relative age structure in terms of trunk diameter classes of Acacia albida trees and shrubs in the Hoanib River, northern Namib Desert region of the Kaokoveld, South West Africa, as reflected by sample transects during 1982.

THE ECOLOGICAL SIGNIFICANCE OF THE DESERT-DWELLING ELEPHANTS

Apart from the elephants' utilization of the vegetation and their obvious impact thereon, this section investigates other factors arising from the elephants' presence in the desert environment as possible indicators of the elephants' influence and place in the general ecology of the region.

Feeding

Feeding observations revealed that the desert-dwelling elephants almost invariably browse by breaking branches or stripping leaves from the trees and shrubs. Occasionally small shrubs were pulled out or kicked out of the ground by a sweeping action of the front foot. Tree-felling, however, seemed to be virtually non-existent as only three uprooted trees, which could be ascribed to elephant action, were seen between 1975 and 1983.

Therefore, the elephants' major mode of feeding (breaking of branches and leaf-stripping) probably resulted in the formation and maintenance of low growing shrubs in the river courses. A notable exception is the tall _Acacia_ trees where the elephants maintain a browsing level beyond the reach of all animals except the giraffe. Most other trees and shrubs in the river courses, however, are kept low by continuous browsing. These low-growing trees and shrubs not only provide food for the low level-grazers, but also act as a refuge for smaller animals and as a reservoir for grass seeds. The latter was conspicuous in 1981 when the only grasses and herbs that reached maturity in the river courses, grew inside the perimeter of the low-growing shrubs while the surrounding area was grazed bare by other herbivores.

The crude pruning effect of the elephants' feeding, by breaking off branches and stripping leaves, stimulates coppicing which lead to an increase in browse production (Barnes 1983), and also reduces the transpiration surface of the plants. As the browsing of woody plants in the river courses usually coincides with the dry seasons, this reduction in transpiration surface could enable the plants concerned to survive on the limited amount of water available during the dry periods. Pruning by elephants also mainly occurred outside the plants' growing period when less photosynthetic products are needed to produce new growth. With the onset of the wet season the elephants move out of the river courses to the flood plains and surrounding areas where they rely mainly on a grass diet (86 per cent of all food taken). The result is that the woody vegetation in the river courses are given a respite from browsing when they enter their growth period.

Elephants are relatively unspecialized herbivores (Laws 1970) and can be regarded as mixed feeders. As mentioned earlier, virtually all plants in the northern Namib Desert, with the exception of the Euphorbia spp., were utilized by the elephants at some stage. This included plants, relatively unpalatable to other large mammals, such as Tamarix usneoides, Phragmites mauritianus, Suaeda plumosa and the exotic weed Ricinus communis. All the latter plants tend to form thickets at the cost of more palatable species. Especially in the flood plains where vast volumes of water accumulate after floods and green plants, notably grass, grow in abundance, the relatively unpalatable plants tend to form dense thickets on the edges of the silt plains where there is better drainage, thus preventing animals from access to the lower-lying areas with an abundance of green grass. By utilizing thicket forming plant species the elephants prevent thicket formation to a large degree. The elephants also opened up paths through these thickets, enabling other large mammals to gain access to food plants and water. In a high rainfall area this might not be so important, but in the northern Namib Desert the flood plains form an important food source for other large animals, especially when it does not rain in the rest of the region.

Seed utilization and germination

Because the elephants apparently show a high feeding preference for the Acacia albida pods of which they eat vast quantities between November and April, tests were done to establish the elephants' influence on Acacia albida seed germination. The seeds themselves seemed to be little affected by the elephant's digestive system and only the pods were digested.

Seeds from freshly-deposited elephant dung and from undigested pods were collected and the two sets of seeds were subjected to germination tests at various time intervals after deposition. The number of seeds from elephant dung and pods which were damaged or parasitised and the number germinating were noted. In undigested pods, 11 per cent of the seeds were parasitised while 17 per cent of the seeds found in elephant dung were either damaged by the chewing action or were originally parasitised. It was not possible to tell the latter difference as all the damaged seeds from elephant dung were partly digested.

Figure 51 is a graphic representation of the germination success of seeds from elephant dung and from undigested pods respectively at various time intervals after deposition. The germination success (58 per cent) of seeds from elephant dung, subjected to the germination tests within one day after dung deposition were significantly higher ($\chi^2 = 83,26$; $p > 0,001$; df=1) than those of undigested pods (only 13 per cent succesful germination). The reason for this is that Acacia seeds have a notoriously hard testa which needs weathering or some sort of damage before water can penetrate (Carr 1976). This hard testa probably accounts for the low germination success of seeds from undigested pods. In fact a large percentage (38 per cent) of the seeds from pods that did germinate were also parasitised and in so doing allowed water to penetrate the testa. Seeds from elephant dung had the testa softened by the elephant's digestive fluids which facilitate water penetration and therefore germination.

However, once the dung had dried out the germination success of

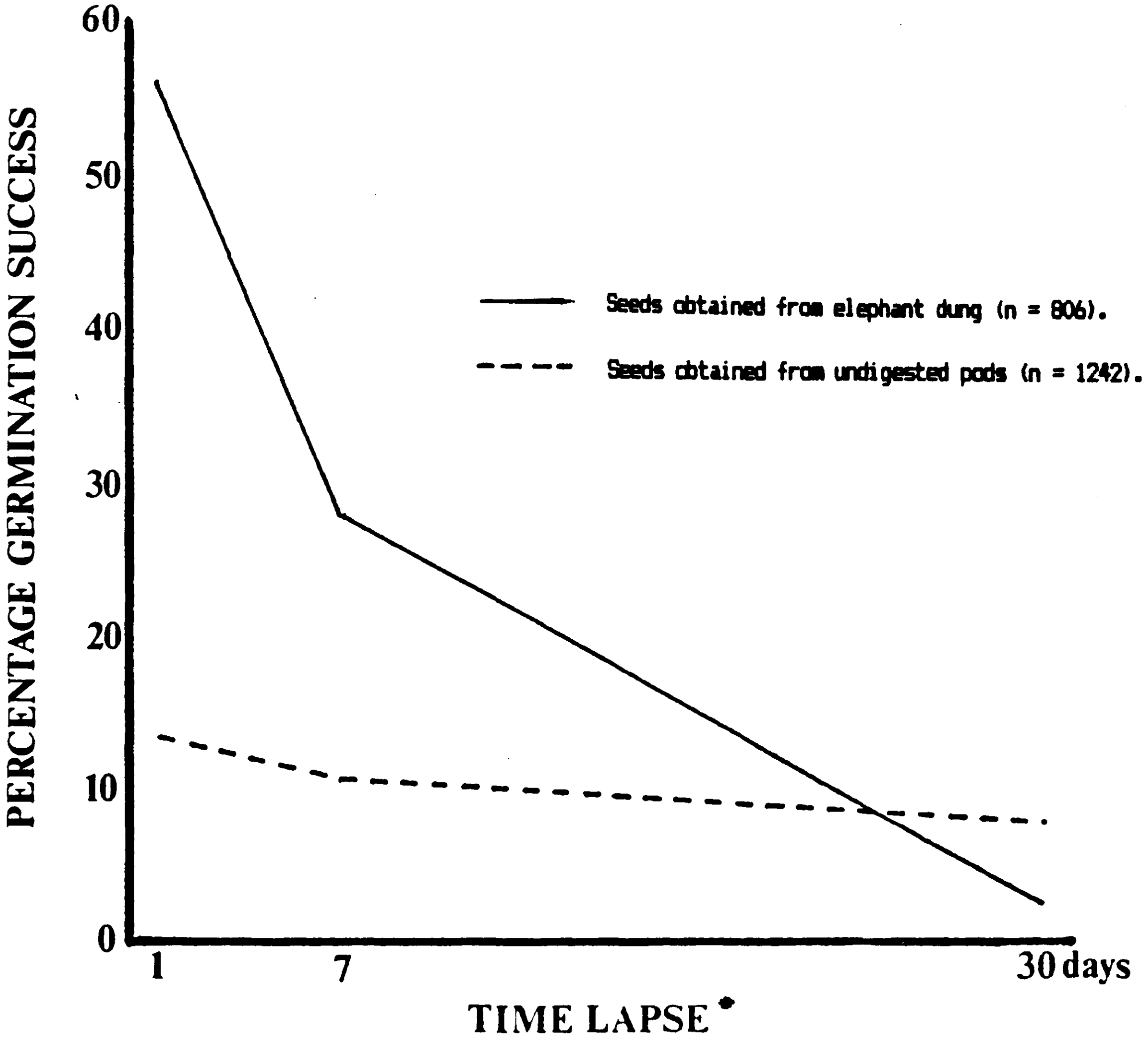


Figure 51: Comparison of the germination success of _Acacia albida_ seeds obtained from undigested pods with those obtained from elephant dung in the Hoanib River, northern Namib Desert region of the Kaokoveld, South West Africa, during 1982. Data are shown on the basis of time lapse since the deposition of dung or the dropping of the pods and the timing of the germination tests involved.

seeds from such dung decreases rapidly. At seven days after dung or pod deposition, 28 per cent of the seeds from dung germinated against 10 per cent from undigested pods. Thirty 30 days after deposition only 2 per cent of the seeds from elephant dung germinated against 7 per cent of those from undigested pods. The reason for this is that seeds in dung partly germinate from the moisture in the fresh dung and then die from a lack of moisture as the dung dries out. Seeds in pods on the other hand remain dormant and will only germinate when the seeds becomes sufficiently wet after the testa was damaged or weathered. The germination success of seeds from undigested pods did not differ significantly between the germination tests (χ^2=1,58; p<0,05; df=2).

Thus, seeds from fresh elephant dung are immediately ready and available for germination and can make optimal use of the short rainy season. The new seedlings' root systems would resist flooding and by the time the soil dried out the seeds from dung could already be established seedlings. The seeds from pods would be unable to germinate with the first rains and during floods would be washed away to the dunes where they will have no chance of survival.

In addition, many other animals, such as the gemsbok and springbok also utilize <u>Acacia albida</u> pods. Na data are available on the germination success of seeds from the dung of these other herbivores but it would be reasonable to assume that the dying-off of partial germinated seeds in the smaller dung of the other herbivores would be more rapid due to a faster drying rate. The larger bulk and thus slower drying rate of elephant dung will ensure that the newly germinated seeds have moisture available for at least three days by which time their roots could have penetrated the soil underneath.

Although many seeds are destroyed by partial germination in elephant or other herbivore dung during dry periods, it must be borne in mind that pod production usually occurs from November to April, a period which largely coincides with the rainy season of March to May. Also the utilization of <u>Acacia albida</u> seeds by elephants and other animals must be seen in perspective with seed production. By using pod production figures for <u>Acacia albida</u> trees in a similar environment, namely the Kuiseb River, central Namib Desert (Van Wyk 1982), and by establishing the mean number of seeds produced per pod and the mean weight of a pod with seeds, the following calculations are possible:-
Each mature <u>Acacia albida</u> tree produces 6 - 33 kg of pods per year. The mean number of seeds per pod is 14,83. The mean weight of a dry pod plus seeds is 6,89 g. The number of pods per kilogramme is 145,14. Thus between 12 914 and 71 030 seeds are produced per tree each year, which is between six and 33 times the total estimated number (2097) of large trees present in the Hoanib River. It is clear that there should be a vast expected excess of seeds available in the Hoanib River each year. Thus the dying-off of seeds in elephant dung might be of secondary importance, the primary advantage might be to have seeds

immediately available for germination during the wet season.

In addition, during the dry season, the seeds in elephant dung is not wasted as many birds such as the red-billed francolin _Francolinus adspersus_, helmeted guinea-fowl _Numida meleagris_ and rock pigeons _Columba guinea_ utilize the seeds in elephant dung. These birds seem to be unable to open up the fresh pods to gain access to the seeds. Especially the francolin seems to rely on this food source during the 1981 drought and were observed to wait patiently for the elephants to defecate after which they immediately scratched open the dung to eat the seeds.

Waterholes

Apart from the Hartmann zebra (most of which either died or migrated east during the drought), and to a lesser extent the black rhinoceros, the elephant was the only other animal in the northern Namib Desert able to dig for its water to a considerable depth. In the sandy river beds, holes which were started by the elephants using the front foot were further excavated by the elephants' trunk up to a depth of 2 metres. In many areas these waterholes dug by the elephants provide the only drinking water for a radius of 40 km or more. Numerous animals obviously depend on these waterholes for survival, and in cases where the sandy holes collapsed, birds and other small mammals could often be seen waiting around these holes for the elephants to return to open them up again.

Open waterholes were sometimes soiled by the elephants wallowing and urinating in them. However, the elephants themselves apparently prefer clean drinking water as they almost invariably dug fresh waterholes next to the soiled ones. As a result there was almost always fresh drinking water available to other animals in such an area.

The likely importance of elephant-dug waterholes to other forms of wildlife can be illustrated from the northern Kaokoveld where the extermination of elephants in 1980 in the Omuhonga River area (Chapter 3) coincided with the disappearance of the black-faced impala _Aepyceros melampus petersi_ in that area. In the vicinity of Okumutati the elephants used to dig and maintain waterholes in the Omuhonga River bed. With the extermination of the elephants in the area this no longer happened and this might well have been one of the reasons for the disappearance of the water dependent black-faced impala in that region.

DISCUSSION AND CONCLUSIONS

The river course forage habitat is clearly the best available habitat for elephants in the northern Namib Desert. It is also the only permanent habitat on which the elephants can depend on for their long-term survival. Flood plains, however, seem to be the most preferred habitat, and all the other habitats, with the exception of the mountains and rocky plains, are utilized on an opportunistic short-term basis only.

As supported by the information gathered on the habitat preferences of the elephants, the highest proportion of woody plants utilized by elephants in the northern Namib Desert are in the river course forage habitat type. The percentages of woody plants utilized by elephants in the mountains and rocky plains forage habitat types outside river courses are negligibly small although a significantly larger proportion of the plants outside river courses that are utilized are killed by the elephants. However, of those woody plants utilized in the northern Namib Desert there are significantly few that are heavily utilized or killed by elephants. Compared to the percentage woody plants utilized by elephants in the eastern savanna forage habitat, a relatively small proportion of the woody plants in the northern Namib Desert are utilized by elephants. The degree of woody plant utilization (elephant utilization classes) is the same in all forage habitat types except in the eastern savanna where a higher percentage of woody plants are heavily utilized or damaged. Elephants are not the major cause of woody plant mortality in the northern Namib Desert. Of all the dead woody plants in the northern Namib Desert, a significant majority are killed by causes other than elephants.

It is clear that the desert-dwelling elephants have a definite preference for certain woody plant species, irrespective of plant availability or size. Emphasis should be placed on those woody plant species with a preference ratio value of more than one as indicators of future trends in the carrying capacity of the region for elephants.

Bark utilization by elephants in the northern Namib Desert affects mainly large _Acacia albida_ and _Acacia erioloba_ trees. In all other tree species it is negligibly small or absent. Most large _Acacia albida_ trees show scars of bark utilization but a relatively small percentage of these is severely damaged or killed. Bark utilization is severe in the vicinity of waterholes (100 per cent of the trees affected) but decreased rapidly in distance from water. After 20 km away from water only 6 per cent of all large _Acacia albida_ trees sampled, are affected. Ring-barking, although seldom encountered, is the major cause of elephant-induced mortality in large _Acacia albida_ trees. The rate of death, however, could not be assessed because of the difficulty in estimating the date of utilization. Photographic records suggest that the data recorded in this study, represents the cumulative bark utilization over a period of more than eight years. The actual ratio of bark utilization per year appears to be low.

There was no significant change in the population of tall trees in the Hoanib River during the last 20 years. There is also no evidence that the elephant population has had any detrimental effect on the population of tall trees. Although earlier aerial photographs are not available for the other large rivers in the region, e.g. the Khumib, Hoarusib and Huab Rivers, these rivers are utilized by only a few elephants (Chapter 3) and the effect of the elephants in the latter rivers should be negligible based on the results obtained for the Hoanib River.

The relative age structure as well as the height classes of <u>Acacia albida</u> plants in the Hoanib River show that all age stages are present. According to Barbour, Bark and Pitts (1980) the reverse J-shaped curve which shows all age stages with many more young plants than old, is characteristic of a climax population. Invading or senescent populations will have either no late age stages or no early age stages. It appears that the <u>Acacia albida</u> population in the Hoanib River is a healthy climax population in which the expected recruitment rate over the long-term will balance the mortality rate.

One fact is immediately apparent when evaluating the ecological significance of elephants in the northern Namib Desert: The present desert-dwelling elephant population has no known detrimental affect on the vegetation of that area. Nor was there any significant damage to the large tree population in the rivers over a 20-year period. In 1969, during an aerial survey, 145 elephants were counted in western Kaokoland (De Villiers 1975), and in 1970 Owen-Smith (1970) estimated the number of elephants in the west to be between 200 and 300. Thus, although there were more than double the present number of elephants in the northern Namib Desert in 1970, even then the results showed no conspicuous destruction of the riverine vegetation. It can only be concluded that the present elephant population is far below the carrying capacity of the northern Namib Desert for elephants and probably has been so for the past 20 years. This is also evident from the 1983 distribution of the desert-dwelling elephants (Chapter 3) where only two river systems, namely the Hoanib and Uniab Drainages were utilized to any degree by the elephants. The remaining large rivers like the Kunene, Khumib, Hoarusib and Huab Rivers has limited utilization and therefore provide room for the expansion of the present elephant population.

Regarding the concern expressed about the elephants' impact on the endemic desert vegetation (Schoeman 1982), the largest proportion of woody plants utilized is in the river courses and with the possible exception of Combretum wattii and Balanites welwitschii (Palgrave 1977), all the plants in the river courses occur in large numbers elsewhere in southern Africa and is more characteristic of higher rainfall regions. The woody vegetation of the larger river courses in the northern Namib Desert is therefore atypical of a desert and is supported by water runoff from the higher rainfall regions in the east. Thus, the woody vegetation of the larger rivers are not endemic to or endangered in that area. The elephants' impact on the vegetation outside the river courses, which can be regarded as typical desert vegetation, is negligible.

The killing of trees by elephants uprooting them as reported elsewhere in Africa (Laws 1970, Spinage and Guinness 1971, Croze 1974b, Caughley 1976, Coetzee, Engelbrecht, Joubert and Retief 1979, Engelbrecht 1979, Jachmann and Bell 1985, Okula and Sise

1986) do not occur in the northern Namib Desert. Whether this is a behavioural characteristic of the elephants or a function of the root systems of the trees is not known.

The only detrimental effect that the elephants might have on the vegetation can be the debarking of large Acacia albida trees in the Hoanib River. Apart from their aesthetic value, these trees are of great ecological value because not only do they provide shade during the hottest months of the year, but the pods which they produce are utilized by a large variety of animals. The ecological importance of Acacia albida trees is regarded as significantly more than its proportional contribution to the primary production of an area (Bourliere and Hadley 1970). As mentioned earlier, however, debarking seems to be an infrequent occurrence and the mortality rate due to debarking is far less than the recruitment rate. Other than in other areas of Africa (Coetzee et al. 1979, Anderson and Walker 1974 and Eltringham 1980), wood borers do not seem to affect live Acacia albida and Acacia erioloba trees in the northern Namib Desert. Even when up to 80 per cent of the bark from a given tree's trunk was removed, wood borers are absent and the trees' are still alive and producing fruits after eight years. At present then, debarking of Acacia albida trees do not seem to be detrimental to the tree population of the northern Namib Desert.

On the other end of the scale, the presence of elephants in the northern Namib Desert seems to be advantageous to the general ecology of the region in the following ways:-

1. During droughts a large number of mammals, birds and insects seems to depend on the waterholes dug and maintained by the elephants.

2. Continuous browsing by elephants keep most trees and shrubs within reach of low-level feeders. The low growing-shrubs also provide a refuge for small animals and act as reservoirs of grass and herb seeds.

3. Browsing stimulates coppicing of trees and shrubs. This can lead to an increase in primary production and possibly also acts as a water conservation measure by reducing the transpiration surfaces of the plants being browsed during the dry seasons.

4. Germination success of _Acacia_ seeds is improved when the seeds are passed through an elephant's digestive system. This process renders the seeds immediately available for germination during the short rainy season.

5. The elephants also eat plants that are relatively unpalatable to other large mammals, preventing thicket formation of these plants at the cost of more palatable plants.

6. The elephants open up paths through thickets to water and choice food spots, enabling other animals to follow. This prevents physical barriers being formed around palatable plants.

7. Seeds in elephant dung seem to be an important food source for game birds, especially during droughts.

In conclusion then, while the elephants apparently have no real detrimental affect on the desert vegetation, their presence seems to be to the advantage of other forms of wildlife in the desert.

Generally, the elephants fit well into the overall ecology of the northern Namib Desert. In fact they must be a vital link in the whole ecology of that area.

In relating the desert-dwelling elephants' survival strategies, it would appear that the river course habitat types are preferred in the dry seasons because of the availability of food there. Permanent water does not seem to be a limiting factor as waterholes, such as at Ganias, with no available food in the vicinity, were mostly avoided during the dry seasons. Also the elephants' high mobility (Chapter 5) results in them being less dependent on the distribution of the waterholes than the other large mammals present in the area. Therefore, food seems to be the major limiting factor of the movements of the desert dwelling elephants during the dry seasons. During the wet season, previously avoided vegetation types such as the flood plains are utilized to a greater extent as they become more suitable as a result of rainfall or river floods. The availability and quality of vegetation seems to be the major factor influencing the habitat choice of the desert-dwelling elephants.

Where the elephants rely on the browsing of trees and shrubs during the hot dry season, they immediately change to grazing during the wet season (86 per cent of the feeding time spent on grazing grasses and herbs). This utilization of grasses and herbs gradually decreases until only 10 per cent of the elephants feeding time during the cold dry season was spent on grasses and herbs. These data illustrate the relatively opportunistic and non-selective nature of the diet of the elephants. This opportunism, together with an elephant's ability to utilize food sources from ground level up to a height of 5 m also was a key factor in the elephants' survival during the 1981 drought. Relatively specialized feeders, such as kudu, gemsbok and zebra (Joubert 1971, Smuts 1972, Dieckmann 1980 and Novellie 1983) are also relatively limited in their feeding height and more than 80 per cent of them died during the 1981 drought (Viljoen 1982b).

CHAPTER 7

OVERALL REVIEW AND MANAGEMENT RECOMMENDATIONS

INTRODUCTION

It is the role of the scientist to provide technical information and to set out possible management alternatives. It is then the role of the manager (and/or politician) to adopt the most appropriate management strategy for the conservation and the utilization of the area concerned (Barnes 1983).

In this chapter results and information pertinent to the conservation and management of the desert-dwelling elephants are reviewed to give an integrated picture of the issues involved. This is followed by specific proposals stemming from the observations during this study on both a long-term and short-term basis.

REVIEW

POPULATION DEMARCATION

Following the argument of Caughley (1977), that a population is a group of interbreeding individuals of the same species having little or no contact with other such groups, the desert-dwelling elephants and the elephants of the eastern areas in the Kaokoveld, each form a distinct population. Apart from their geographical separation, each of these two populations has separate movement patterns, climatic regimes and adaptational requirements. It is concluded that the eastern and desert-dwelling elephant populations are naturally isolated, following the pattern of many other African elephant populations (Chapter 4).

However, due to the veterinary fence in Damaraland, the classification of some elephants as members of a transitional elephant population is regarded as artificial, especially in the south-west of their distribution range. In the east and north-east, the transitional population's distribution range and movement patterns indicate a natural segregation from the eastern elephant population. Also, between Sesfontein and Palmwag the transitional population appears to be naturally isolated from the desert-dwelling elephant population. In the south-west, however, between Palmwag and Wêreldsend, these elephants' movements are restricted by the veterinary fence. To a large extent this portion of the fence follows no ecological boundary or pattern; especially so between Wêreldsend and Juriesdraai where it follows a haphazard pattern which appears to be more a result of ease of erection than anything else.

This fence probably cuts through the home ranges of some elephant groups which might originally have been members of the desert-dwelling population, as indicated by the following observations: Between 1980 and 1981 several unsuccessful attempts (n = 16) were witnessed of family groups from the transitional population trying to break westward through the fence. There were no attempts from members of the desert-dwelling elephants to break eastward through the fence. Also, sporadic movements (n=3) by individuals of the transitional population along the southern boundary of the fence as far west as Springbokwasser during 1981, might indicate their original movement patterns. During the excessive floods in 1982, large portions of the veterinary fence were washed away and a number of the transitional elephants moved through these gaps and made contact with the desert-dwelling elephants. With the subsequent repairing of the fence some of these elephants (±20) were then "trapped" west of the fence and were apparently unable to move back. It is concluded that although the majority of the elephants in the transitional population are probably correctly classified, some members of the latter population might originally have been part of the desert-dwelling population. However, with the fence now governing their movements, such a conclusion remains speculative. Despite this shortcoming, the three elephant populations of the Kaokoveld must still be regarded separately when assessing densities, stocking capacities and management.

POPULATION VITALITY AND LIMITING FACTORS

There is no evidence from the results in this study to support a hypothesis that the desert-dwelling elephants represent an anomalous population which was forced into an unsuitable habitat (Schoeman 1982). All previous records indicate that elephants were present in the desert long before the advent of western man and the elephants' present distribution and movements in relation to human occupation of the region suggest that they occupy the desert habitat voluntarily (Chapter 3).

Although environmental conditions in the desert influence recruitment rate and are probably the main cause of a degree of increase in age at sexual maturity and mean calving interval in the desert-dwelling elephant population, these parameters are still within the limits of other elephant populations in Africa. The social organization, social structure, sex ratio, age structure, movement and feeding patterns of the desert-dwelling population also correspond largely with that of other elephant populations in Africa (Chapter 4). The age and sex structure of the desert-dwelling population also indicate that this population is still viable. There is thus no indication that the desert environment has a marked adverse affect on the vitality or condition of the population concerned.

Recruitment rate fluctuated according to environmental conditions during the year of conception, but the mean recruitment rate over a period of time remained relatively constant, showing no apparent change in fecundity between the periods 1977 to 1981 and 1982 to 1986 (Chapter 4). Thus a high mortality rate and not a reduction in fecundity was the major cause of decline in the desert-dwelling elephant population up to 1982. From carcass counts, mortality caused by illegal hunting was decidedly the major population limiting factor of the desert-dwelling elephants. The immediate priority for the conservation of the desert-dwelling elephants should thus be the elimination of illegal hunting.

Apart from illegal hunting, disturbance has an incalculable but probably also a serious influence on the survival of the elephants and other game in the region. Following the recent spate of publicity on the Kaokoveld, there is an increasing number of tourists visiting the area in four-wheel-drive vehicles. This gives rise to trampling of vegetation, litter, game chasing and denying game access to water by camping at waterholes. The easiest route for vehicles is usually down the dry river courses and because of the narrow gorges in which most rivers flow, vehicles driving down these rivers not only trample tree seedlings but also cause immense disturbance by chasing animals (deliberately or not) for long distances down the narrow gorges. There are three confirmed cases of elephant deaths resulting from disturbance in one or other form. However, the indirect influence of disturbance on reproduction is probably more serious as the elephants' mating season is usually restricted to the short wet season, and any disturbance during this period might have a far-reaching effect on the calving rate.

If illegal hunting is stopped and disturbances are limited, it is believed that the desert-dwelling elephants would initially increase through a high growth rate due to the relatively unutilized environment, as was experienced in the Addo National

Park (Hall-Martin 1980).

ADAPTATION

From the results in this study the desert-dwelling elephants appear to be well adapted to the desert environment. Furthermore, these elephants probably provide a vital link in the general ecology of the desert through their water digging habits and feeding modes. These elephants, together with the giraffes and black rhinoceroses survived the recent drought conditions better than the other large mammals in the northern Namib Desert. Although apparently not divergent from other elephants in Africa, the desert-dwelling elephants make optimum use of an elephant's natural capabilities in order to survive in the desert. Their mobility, intimate knowledge of resource distribution in the desert and ability of going for extended periods without drinking water are the primary keys to their survival. Knowledge of resource distribution within the desert appear to be vital, making any attempts at repopulation through the translocation of elephants from elsewhere questionable.

Although scarce and scattered, the location of waterholes in relation to feeding grounds are well within the capabilities of the desert-dwelling elephants. Thus management emphasis should be on the protection of the elephants from human predation and disturbance and on the continued availability of natural resources, rather than on the improvement of the habitat.

VEGETATION UTILIZATION AND CARRYING CAPACITY.

The data presented show that the present number of desert-dwelling elephants has no detrimental affect on the desert vegetation. Monitoring of vegetation through aerial photographs, and the relative age structure of large trees in the river courses also suggest that for at least the last 20 years these elephants have had no marked detrimental affect on the large trees in the desert.

Detailed data on the vegetation biomass, primary production and elephant food requirements in the desert are not available. Thus it would be difficult to establish the maximum number of elephants that could be sustained by the desert without damage to the environment. However, it is possible to predict the potential carrying capacity from simple meteorological data (Coe <u>et al.</u> 1976) in terms of large herbivore standing crop per km^2, using the equation :

$$\mathrm{Log}_{10}\text{Large Herbivore Biomass (kg)} = 1{,}685 \times \mathrm{Log}_{10}\text{Annual Rainfall (mm)} - 1{,}095$$

Since the study area encompass a marked rainfall gradient from east to west, an overall mean rainfall figure of 63,55 mm per annum for the northern Namib Desert was calculated by using the mean annual rainfall figures from Möwebaai (19,0 mm per annum) and Sesfontein (108,1 mm per annum). These stations are situated on the western and eastern boundaries of the northern Namib Desert respectively. Substituting the overall mean annual rainfall in the formula above gives a predicted large herbivore standing crop of 87,75 kg per km^2 for the northern Namib Desert. The 1983 distribution range of the desert-dwelling elephants cover an area of 14 750 km^2, giving a predicted total large herbivore biomass (87,75 x 14750) of 1 294 312,5 kg for the area. To determine the proportion of each large herbivore species, including the ostrich (Struthio camelus), in the total biomass, the total numbers counted in all available aerial surveys in the northern Namib Desert (Visagie 1977, Le Roux 1978, Viljoen 1982b), were summed and the mean proportion of each species calculated. Then by using the unit mass figures given by Coe et al. (1976) and that of Smit (1964) for the ostrich, the percentage contribution of elephant biomass to the total biomass was calculated at 22,6 per cent. This gives a predicted elephant biomass of 292 514,6 kg for the 1983 distribution range, which is equivalent to 0,01 elephants per km^2 or 169 elephants. In 1977 the range of the desert-dwelling elephants covered an area of 20 290 km^2, and with a suggested crude elephant density of 0,01 per km^2 this would amount to 233 elephants.

This can only be approximate estimates, but Coe et al. (1976) regarded their equation as a conservative prediction of biomass which is probably closely related to the long-term carrying capacity of wildlife areas. Also primary production in the northern Namib Desert is probably higher than indicated by the annual rainfall as a result of water run-off from the higher rainfall areas in the east. This would raise the large herbivore carrying capacity of the desert above that predicted by annual rainfall. Thus, for present management purposes, it is proposed that an elephant density of 0,01 per km^2 or between 169 and 233 elephants (depending on their distribution range), be considered the maximum number of elephants which can be sustained by the desert without permanent damage to the vegetation. According to the data presented in chapter four, this density will only be reached after the year 2000 under conditions of adequate protection.

CONSERVATION STATUS

The mobile nature of the African elephant and its long generation time make it unlikely that any elephant population within southern Africa could have been isolated long enough for any significant genetic differences to become established. Elephants in southern Africa are regarded as being from the same basic genetic stock (Osterhof, Young and Ward-Cox 1972, Fairall 1982) as until relatively recently there was a virtual continuous distribution of elephants throughout southern Africa (Roberts 1951, Skead 1980, Smithers 1983). The desert-dwelling elephants of the northern Namib Desert are therefore not regarded as a separate subspecies and they are probably still related to the elephants of the Etosha National Park by genetic exchange via the transitional elephant population.

However, having said that, it would be surprising if all elephant populations in southern Africa are still genetically identical because of the vast differences in environmental pressures and therefore in the survival requisites of the different elephant populations in different environments. In the northern Namib Desert, for example, an individual elephant's survival will depend on its ability or tolerance to go for long periods without drinking water and to move over vast distances between food and water. On the other hand, both food and water are relatively abundant in the Etosha National Park and the above-mentioned abilities will not be so important for an individual elephant's survival. Over a long period of isolation and through the process of survival of the fittest, this might eventually result in genetic differences between elephant populations, especially, with artificial human-introduced barriers between elephant populations. Also, the establishment of discrete unit elephant populations resulting from restricted movement patterns, indicates that there may be a temporary or short-term genetic isolation.

Nevertheless, although the desert-dwelling elephants cannot be regarded as a subspecies of Loxodonta africana, they represent an ecotype which illustrates the ultimate capacity of the African elephant to adapt to marginal conditions. As far as could be established, there are only two other regions in Africa where elephants exist under similar conditions. These are in Mali and Mauritania on the edge of the Sahara Desert (Douglas-Hamilton 1980, Bosman and Hall-Martin 1986, Guillemont 1986). However, the climatic regime of those elephants in Mali and Mauritania appear to be more on par with that of eastern Kaokoveld (Grove 1971).

In 1982 the International Union for Conservation of Nature and Natural Resources (IUCN) declared the desert-dwelling elephants of the northern Namib Desert a conservation priority (Jackson 1982). As elephants alone they are not that important, they can equally be preserved in a zoo, but together with animals such as the giraffe, black rhinoceros and the large variety of other mammals, birds, endemic plants, reptiles and insects in a desert renowned for its topographic grandeur, these elephants form an important component of an unique ecological entity which is found nowhere else in the world. By ensuring the survival of the desert-dwelling elephants in their natural environment we will automatically conserve a whole spectrum of desert ecology.

Apart from the obvious aesthetic and scientific importance of the desert-dwelling elephants, the conservation of ecotypes as far as possible in their historical, geographical or topographic locations is regarded as essential to maintain genetic variability. This in turn will improve the flexibility or adaptability of the species involved in the long term (Comrie Greig 1979). To try and replace the desert-dwelling elephants by other elephants through translocation, as Comrie Greig (1979) pointed out, will defeat the aims of genetic conservation. If we allow the desert-dwelling elephants to become extinct, an unique ecotype will be lost forever.

MANAGEMENT RECOMMENDATIONS

Various recommendations and proposals regarding the conservation and management of the Kaokoveld area has been submitted (Owen-Smith 1970 and 1972, Tinley 1971, Joubert 1972, Page 1976, Eloff _et al._ 1977, Anon 1980). All these reports emphasize the ecological importance and the conservation priority of the Kaokoveld, especially the western regions, and not one of the proposals have yet been implemented. It is beyond the scope of this study to discuss each of the above-mentioned proposals in detail and the recommendations related below should be seen as being in accordance with the previous recommendations. Rather than presenting a detailed management plan, such as that which is described in the report of Eloff _et al._ (1977), only those salient factors deemed necessary for the conservation of especially the elephants, will be highlighted here.

SHORT-TERM MANAGEMENT RECOMMENDATIONS

In anticipation of a clearly defined policy regarding a future nature reserve and its management in the northern Namib Desert region, the recommendations related below are considered essential for the immediate survival and conservation of especially the desert-dwelling elephant population of the region. Since the environment does not appear to be a limiting factor at present, the recommendations below are mainly aimed at reducing the human-elephant conflict.

Law enforcement

As illustrated previously, illegal hunting is the single most jeopardizing factor for the survival of the desert-dwelling elephants and effective anti-poaching measures as well as measures to reduce disturbance, are essential and immediate prerequisites.

The vastness and inaccessible nature of large tracts of the Kaokoveld make it difficult to impossible to patrol the area efficiently and the following measures are proposed to increase the competence of law enforcement:

1. At least six experienced nature conservation officers are required (regarded as the absolute minimum) to patrol the Kaokoveld efficiently.
2. A spotter aircraft and a pilot which can be regularly used for anti-poaching as well as game monitoring patrols should be permanently available in the region . In this respect the private sector can be approached for the donation and maintenance of such an aircraft.
3. The use of auxiliary game guards, working on a bonus system, appear to work efficiently (Owen-Smith 1986) and should be encouraged.
4. Vehicular traffic, official or otherwise, should be limited and controlled. To achieve this end, the erection of vehicle-proof barriers at entrance points to the Hoanib River is proposed: Because of the mountainous terrain and the veterinary

fence all vehicles are forced to use one of eight routes to enter the western course of the Hoanib River and the area south of it. All these routes pass, at some stage, through narrow gorges (the widest being 150 m and most of the others being less than 50 m wide) where there is no bypass. Vehicle-proof barriers can be erected at those points by planting sections of railway line upright across the width of the narrowest part of the various gorges. In order to stop any vehicle effectively (with the exception of motorcycles), these metal posts need only to be 0,75 m high and spaced 1,5 m apart without any interconnecting wires or poles. This will not restrict the movements of any animal and will not be damaged by flood waters. By concreting these posts into the ground, they will be virtually indestructible. Access to the area can be through the Skeleton Coast Park or through key-controlled gates. Such vehicle-proof barriers will have the following advantages:

a. The whole western Hoanib River, the area south up to the Uniab River as well as a portion of the Skeleton Coast Park, will be effectively protected against any unauthorized vehicle.

b. The animals in these areas will be protected from virtually all poachers and disturbance.

c. The proposed barriers will not restrict the movements of any animal.

d. Although the local people have up to now largely avoided the proposed enclosed area, the barriers should be acceptable to them as it will not restrict their movements (on foot or horseback, as is their tradition).

e. Fewer personnel will be needed to control these areas and it will relieve the working pressure of the present personnel.

f. The proposed barriers will be relatively cheap (compared to extra personnel, vehicles or fences) and will require no maintenance.

g. For a small capital outlay and little effort a large area can thus be effectively controlled.

Water availability

Natural waterholes which lasted throughout the 1977-1981 drought appeared to be sufficient in number and adequately spaced and well within the range of desert-dwelling elephants. It is recommended that no artificial water points be made in the northern Namib Desert. Artificial waterholes would only encourage invasion by domestic animals as well as the build-up of game populations above the natural carrying capacity of the region with the resultant overgrazing and habitat deterioration.

However, one major problem is the continuous accessibility of the permanent waterholes to game. At the Orupembe, Sanitatas and Dubis waterholes, game are sometimes denied access to the water by means of thornbush fences and the lighting of fires by cattle owners. Also some visitors to the region tend to camp at and wash with detergents in these waterholes, thus denying game access to the water for several days as well as polluting the water. During droughts, even one extra day without water could be fatal to some game. Thus, rather than extra water points, priority should be given to ensure the continuous availability of waterholes to game and this approach should be enforced if necessary.

Veterinary fence

Although the present location of the veterinary fence in Damaraland is a marked improvement on the originally proposed location, it is still largely incompatible with the movement patterns of elephants and other game. Because the fence imposes restrictions on the elephants' natural movement patterns, the elephants in this area are inevitably forced to clash with the farming activities in the area.

It is proposed that the section of the fence between Wêreldsend and Palmwag (approximately 40 km of fence), be moved east up to the watershed on the farms Wêreldsend, Spaarwater, Juriesdraai and Palmwag. The additional areas (approximately 30 000 ha) thus enclosed west of the veterinary fence is at present uninhabited by humans and to a large extent unutilized by the farmers in the area. In affect some 30 to 40 members of the transitional elephant population will then be enclosed west of the fence which would be more compatible with the movement pattern and affinities of these elephants. More important , however, is that for the elephants it would mean better protection against poaching while at the same time it would protect the farmers on the farms Bergsig, Palm, Spaarwater and Fonteine against elephant damage to their installations and crops. With the existing location of the fence the unavoidable conflict between the farmers and the elephants will continue and the transitional elephant population will gradually be reduced as "problem" elephants are shot. Thus with a relatively small alteration of the veterinary fence, which will not interfere with the present land-use of the area, the farmers as well as the elephants will benefit which will be more economic in the long run.

Furthermore, the section of the veterinary fence between Wêreldsend and Torra Baai is totally unacceptable as it cuts through a proclaimed nature reserve and blocks the north-south movements of game in the Skeleton Coast Park. It is proposed that this section of the fence to be totally removed. If necessary, it can be linked up with the proposed location of the fence at Wêreldsend and then extend south in correspondence with the boundaries of a possible future nature reserve.

LONG-TERM RECOMMENDATIONS

The obvious and only long-term solution for the conservation of the northern Namib Desert ecology, would be the declaration of the entire region as a natural conservation area with the proper control and management. Justification for such a reserve cannot be based on the aesthetic value or the wilderness concept as it is unacceptable in the present milieu of Africa. Economic considerations alone will determine the survival of many wildlife areas in the long run (Hanks 1979). Fortunately, although the aesthetic and scientific value of the northern Namib Desert are unequalled, there is also sound economic reasons for the conservation and management of the region as a conservation area. The northern Namib Desert region is virtually uninhabited by humans, unsuitable for any form of agriculture and has little mining potential (Loxton _et al._ 1974 a and b, Page 1976). The only viable source of income from this region for the people of the Kaokoveld would be through tourism and the associated job opportunities and possibly also from controlled trophy hunting and game harvesting. However, in spite of numerous proposals (Owen-Smith 1970, Tinley 1971, Joubert 1972, Page 1976, Eloff _et al._ 1977, Anon 1980) such a nature reserve has not yet materialized. It would appear that the major stumbling block in the path of such a reserve is of a political nature rather than sound practical reasons.

Thus, in order to succeed, the boundaries of any proposed nature reserve in the region must be a compromise between the ideal ecological unit and political issues. Fortunately, the agricultural potential of the Kaokoveld spontaneously imposes a boundary between the economically viable areas and those which would be suitable for a nature reserve (Page 1976). Figure 52 depicts the boundaries of such a proposed nature reserve in the Kaokoveld. Although largely similar to that of previous proposals, it is a compromise in that it only contains the region with the least effective human living area in the Kaokoveld.

The eastern border of the proposed reserve roughly follows the

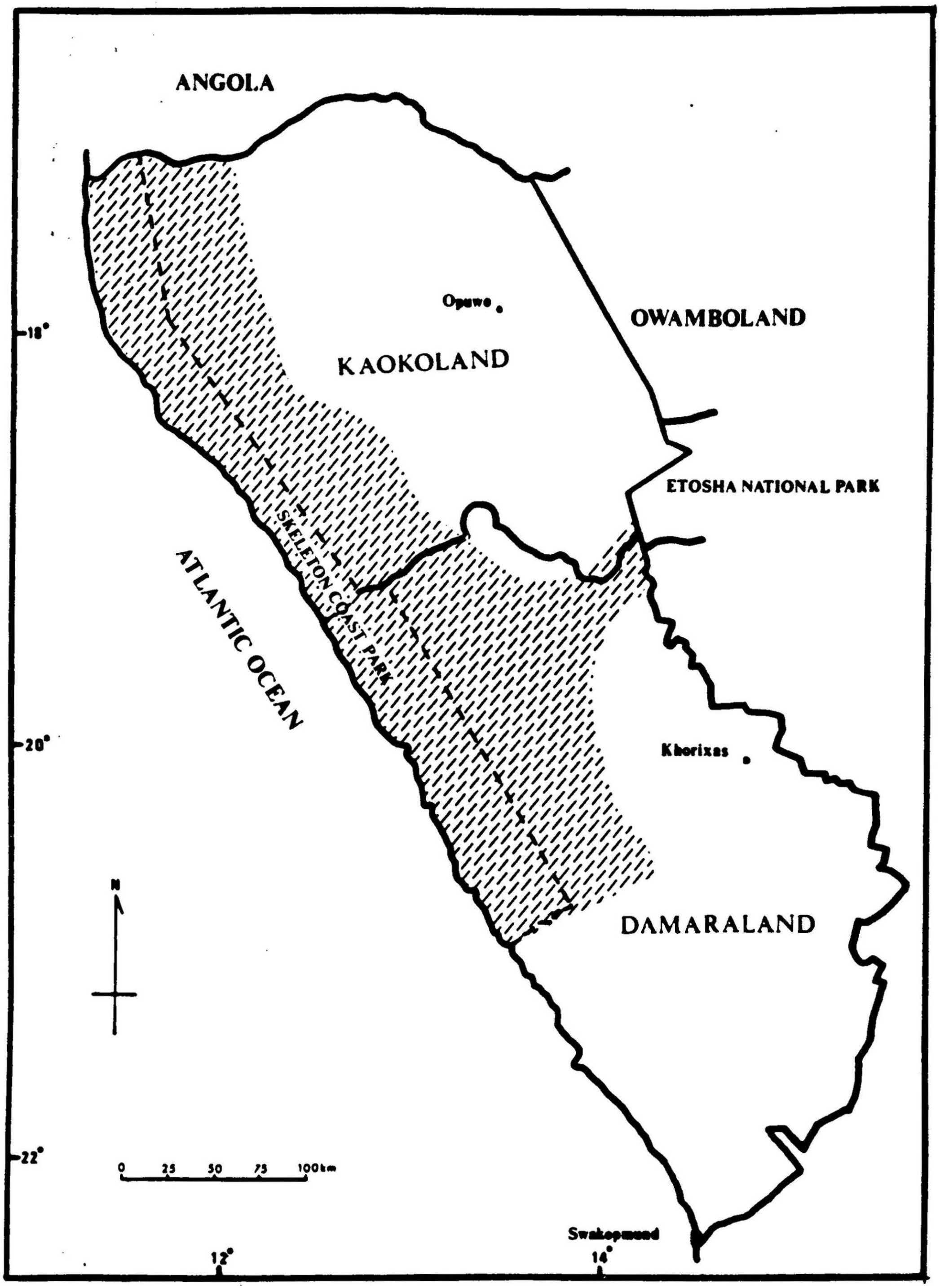


Figure 52: Proposed northern Namib Desert Nature Reserve (shaded area) in the Kaokoveld, South West Africa. The proposed area is a compromise between the ideal ecological unit and present human occupation and land-use forms in the Kaokoveld.

100 mm isohyet in Kaokoland, extending to the 150 mm isohyet in Damaraland. Starting at the Otjihipa Mountains in the north, the boundary extends south towards the Gomatum River to include the Otjiha Plains and the valleys east of Sanitatas. Thence it extends south-east to include the Giribes Plains and Dubis Waterhole south of Sesfontein. It continues easterly, staying south of the permanent human settlements at Sesfontein and Warmquelle to link up with the Etosha National Park north of Otjovasando. From the south-eastern corner of the Etosha National Park it follows the boundary of the present veterinary fence up to Otjihavera whence it extends south along the watershed west of the Bergsig-Palm road, as previously proposed, up to Die Riet. Thereafter it follows the original farm boundaries up to the Ugab River in the south. Ideally, the proposed reserve should also extend southward to the Swakop River to include the Brandberg and Spitskoppe.

Although the Kaokoland region of the proposed reserve is exploited from time to time by nomadic pastoralists, it should pose no threat to the conservation of the region provided that the populations of man and stock are small and mobile, the game is not denied access to waterholes and that hunting is restricted for own consumption. The only (recent) permanent human settlement causing a problem within the proposed reserve is at Purros. Situated in a narrow gorge in the Hoarusib River, this settlement restricts game movements up and down the river resulting in an unavoidable human conflict with predators and elephants. In 1981 the people residing at Purros had to receive famine aid (Anon 1981), illustrating the unsuitability of the region for permanent human occupation. It is proposed that an alternative livelihood, outside the proposed reserve, be offered to the people at Purros which would be an improvement on their current subsistence living level.

Although not the ideal ecological unit it is believed that the proposed reserve (Fig. 52) will be viable, not only for the survival of the desert-dwelling elephants but also for the whole spectrum of their environment. The link to the Etosha National Park will ensure the continued existence of the known migratory animals such as the Hartmann' mountain zebra (Viljoen 1982a), and it will probably also solve most of the current problems associated with overgrazing in western Etosha as well as the movements of elephants from the Etosha National Park into eastern Kaokoveld. The proposed reserve, if properly managed, will make a valuable contribution to the economy of the Kaokoveld which can help to replace the current subsistence living level of most of the local inhabitants. Negligence and continued protracted petty arguments over the conservation status of the desert-dwelling elephants and their environment will inevitably lead to their extinction, a point only too well illustrated by the current plight of the Knysna elephants.

It must be emphasized that the delineation of the boundaries of a nature reserve and the prevention of hunting, agriculture or other industry within those proposed boundaries, is in itself not enough. The *raison d'être* of such a reserve must be clearly defined and the conservation objectives as well as the economic value must be brought to the attention of the local people through positive education. In a developing country the immediate economic considerations are likely to be of overriding importance and unless the people of the Kaokoveld get a tangible advantage from it, the survival of the natural habitats and their wildlife will not be ensured. This does not mean that aesthetic and ecological factors, because their benefits are often indirect without apparent economic value, are unimportant. In the long run the converse might be true.

Equally important for the survival of wildlife areas is a long term land-use policy for the surrounding areas which should be based on an integrated land-use system with the objective of optimizing economic, cultural and conservation values. It is a fallacy to believe that a nature reserve can survive or its boundaries respected while the surrounding areas suffer from mismanagement, habitat degeneration and poverty. It is proposed that future research should be aimed at formulating viable land-use systems for the optimum long-term utilization of all natural resources in the eastern Kaokoveld.

SUMMARY

This study was carried out in the Kaokoveld, South West Africa. The Kaokoveld encompasses the political areas of Kaokoland, Damaraland and the Skeleton Coast Park and covers approximately 11 million hectares. It has a marked rainfall gradient from 350 mm per annum in the east to as low as 19 mm in the west. The vegetation ranges from a <u>Colophospermum mopane</u> savanna in the east to a sparsely vegetated desert in the west where plants are mainly restricted to the dry water courses. Topographically the area is mountainous, intersected by large broken valleys with sandy, gravel or stony plains predominant in the west. The drainage is well defined with dry river courses draining mainly from east to west.

The elephants of the Kaokoveld are divided into three populations, namely a western or desert-dwelling population, an eastern population and a transitional population. In 1983, 357 elephants were counted in the Kaokoveld with 70 in the desert-dwelling population, 207 in the eastern population and 80 in the transitional population. Currently the elephants' status seems to be relatively stable following intensified law enforcement. However, with the small population sizes, the situation remains vulnerable.

The study was mainly directed at the desert-dwelling elephant population whose focus of distribution is in the western Kaokoveld, also known as the northern Namib Desert. Covering

approximately 4,5 million hectares, the northern Namib Desert is extremely arid, receiving less than 150 mm of rain per annum. Available records indicate that the desert-dwelling elephants were present in the northern Namib Desert long before the advent of western man and the elephants' present distribution and movements in relation to human occupation of the region suggest that the elephants occupy the desert habitat voluntarily.

The advanced social system of the African elephant, as manifested in the desert-dwelling elephant population, make these elephants well equipped to cope with the adversities of an arid environment. The basic unit of the desert-dwelling elephants' social organization is the family unit, consisting of cows and calves of all ages and young males up to the age of 17 years. The stability of each family unit in terms of numbers, structure, movement coordination and home range remained predictably stable throughout the study period. Mature elephant bulls generally show no affinity with any one family unit or with other individual bulls. Bull groups are unstable and their numbers and composition fluctuate frequently.

The age distribution of the desert-dwelling elephants shows a large variation in age-class sizes. The variation in the younger age-class sizes is attributed to a variation in recruitment rate since the data do not support the occurrence of a clear age-specific mortality. Recruitment was clearly related to the amount of rainfall recorded during the year of conception. The sex ratio of the desert-dwelling elephant population shows a parity in animals up to 15 years of age but the sex ratio of older animals differs significantly from parity, indicating a sex-specific mortality in favour of females in the older age classes. This is attributed to selective hunting for the large tusks of bull elephants. Environmental conditions are probably the main cause of an apparent increase in age at sexual maturity and mean calving interval in the desert-dwelling elephant population. However, these parameters are still within the limits of other elephant populations in more suitable habitats elsewhere in Africa.

The internal structure of the desert-dwelling elephant population indicate that the population is still viable and there is no indication that the desert environment has a marked adverse affect on the vitality or condition of the population concerned. A high mortality rate and not a reduction in fecundity was the major cause of decline in the desert-dwelling population up to 1982. From carcass counts, mortality caused mainly by illegal hunting was decidedly the major population limiting factor in the desert-dwelling elephants. In the absence of human-induced mortality it is predicted that the desert-dwelling population will double by 1997 to reach a size of 140 elephants.

All movements of the desert-dwelling elephants, including occasional wanderings up to 195 km, were confined to the northern Namib Desert and no evidence could be found of any movements including migrations to and from the Etosha National Park. The main feature of the desert-dwelling elephants' spatial strategy is the marked fidelity to individual home ranges. The mean daily distance moved by these elephants is 25,7 km. This mobility, together with their ability to stay for up to 96 hours without drinking water enable the elephants to utilize food sources up to 68 km away from waterholes. The elephants' mobility, intimate knowledge about resource distribution within their home ranges and ability to go for extended periods without drinking water, are regarded as key factors in the survival of these elephants in the desert.

Dry river courses are the best available habitat for elephants in the northern Namib Desert and also form the only habitat on which the elephants can depend on for long-term survival. Flood plains seemed to be the most preferred habitat and all other habitat types are utilized to a lesser degree. Presented data show that the present number of desert-dwelling elephants has no detrimental affect on the desert vegetation. Monitoring of aerial photographs as well as the relative age structure of large trees in river courses also suggest that for at least the last 20 years these elephants have had no marked detrimental affect on the population of large trees of the desert. Detailed information on the desert carrying capacity is not available but by using meteorological data, the potential carrying capacity can be calculated in terms of large herbivore biomass. This suggest an elephant density of 0,01 per km^2 which can be sustained by the desert without permanent damage to the vegetation.

Although apparently not genetically divergent from other elephants in Africa, the desert-dwelling elephants of the northern Namib Desert make optimum use of an elephant's natural capabilities to survive in the desert. From the results in this study the desert-dwelling elephants appear to be well adapted to the desert environment. Furthermore, these elephants probably also provide a vital link in the general ecology of the desert through their water digging habits and feeding modes. The presumably unsuitable desert habitat appears to be a minor population limiting factor at present. Thus, short-term management recommendations to ensure the immediate survival of these elephants, must be aimed at reducing human-elephant conflict rather than habitat improvements. Conservation measures, such as the elimination of illegal hunting, reducing of disturbance, continuous availability of waterholes, controlling vehicular traffic and the relocation of the veterinary fence, are proposed to this effect.

In the long-term, the only permanent solution to ensure the conservation of the northern Namib Desert ecology, will be the declaration of the region as a nature reserve with the proper control and management. The proposed boundaries of such a reserve are a compromise between the ideal ecological unit and socio-economic and political issues. The desert-dwelling elephants of the northern Namib desert represent an unique ecotype of _Loxodonta africana_ which is not only of aesthetic, scientific and ecological importance, but also of potential economic value to the region.

OPSOMMING

Hierdie studie is in die Kaokoveld, Suid Wes-Afrika uitgevoer. Die Kaokoveld sluit die politieke gebiede van Kaokoland, Damaraland en die Skedelkuspark in en is ongeveer 11 miljoen hektaar groot. Die gebied het 'n opvallende reënvalgradient vanaf 350 mm reën per jaar in die ooste tot so laag as 19 mm in die weste. Die plantegroei wissel van 'n <u>Colophospermum mopane</u> savanna in die ooste tot 'n woestyn met ylverspreide plante, hoofsaaklik tot die rivierlope beperk, in die weste. Topografies kan die gebied as bergagtig, afgewissel met gebroke valleie, en met sanderige, gruis en klipvlaktes oorheersend in die weste, beskryf word. Die dreinering is goed gedefinieer met droë rivierlope wat van oos na wes dreineer.

Die olifante van die Kaokoveld word in drie bevolkings, naamlik die westelike of woestynlewende bevolking, die oostelike bevolking en die oorgangsbevolking, verdeel. In 1983 was daar 357 olifante in die Kaokoveld, met 70 in die woestynlewende bevolking, 207 in die oostelike bevolking en 80 in die oorgangsbevolking. Huidiglik, na meer intensiewe wetstoepassing, lyk die olifante se getallestatus relatief stabiel, maar met die steeds lae olifantgetalle bly die toestand kwesbaar.

Die studie was hoofsaaklik op die woestynlewende olifantbevolking gerig. Hierdie olifante se verspreidingsgebied is in die weste van die Kaokoveld, ook bekend as die noordelike Namib, gekonsentreer. Die noordelike Namib is ongeveer 4,5 miljoen

hektaar groot en met minder as 150 mm reën per jaar, word dit as uiters droog beskou. Beskikbare inligting dui daarop dat die olifante die woestyn lank voor die koms van die blanke reeds benut het. Die olifante se huidige verspreiding en bewegings ten opsigte van menslike besetting van die gebied is 'n aanduiding dat die olifante die woestyngebied uit eie beweging beset.

Die gevorderde sosiale sisteem van die Afrika-olifant, soos geopenbaar deur die woestynlewende olifante, maak dat hierdie olifante goed vir die uiterste toestande van die woestyn toegerus is. Die basiese eenheid van die olifante se sosiale organisasie is die familie-eenheid, wat uit koeie en kalfies van alle ouderdomme en jong manlike diere, tot 17 jaar oud, bestaan. Die stabiliteit van elke familie-eenheid in terme van getalle, struktuur, bewegingskoördinasie en tuisgebied, het deurentyd gedurende die studie tydperk voorspelbaar dieselfde gebly. Volwasse olifantbulle het oor die algemeen geen affiniteit vir enige spesifieke familie-eenheid of ander individuele bulle getoon nie. Bulgroepe was onstabiel en hulle getalle en samestelling het deurentyd verander.

Die ouderdomstruktuur van die woestynlewende olifantbevolking toon 'n groot variasie in ouderdomsklasgroottes. Hierdie variasie word aan 'n variasie in geboortetempo toegeskryf, aangesien die beskikbare inligting nie ouderdomspesifieke mortaliteit aandui nie. Die geboortetempo was duidelik gekoppel aan die hoeveelheid reënval gedurende die jaar van bevrugting. Die geslagsverhouding van olifante tot op die ouderdom van 15 jaar was gelyk, maar in die ouer diere is daar 'n betekenisvolle afwyking van 'n gelyke verhouding. Dit dui op 'n geslagspesifieke mortaliteit ten gunste van olifantkoeie en word aan 'n jagseleksie vir die groter ivoortande van olifantbulle toegeskryf. Omgewingsfaktore is waarskynlik die hoofoorsaak van 'n klaarblyklike toename in ouderdom by geslagsrypheid en gemiddelde kalfinterval in die woestynlewende olifantbevolking. Nietemin is hierdie parameters nog binne die bestek van die van ander olifantbevolkings in Afrika.

Die interne struktuur van die woestynlewende olifantbevolking dui daarop dat die bevolking nog steeds lewensvatbaar is en daar is geen aanduiding dat die woestynomgewing 'n merkbare negatiewe invloed op die betrokke bevolking het nie. 'n Hoe mortaliteitstempo en nie 'n verlaging van vrugbaarheid nie, was die hoofoorsaak van die bevolkingsafname tot 1982. Deur karkasondersoeke was dit duidelik dat hierdie hoe mortaliteit hoofsaaklik deur onwettige jag veroorsaak was. Onwettige jag is die grootste beperkende faktor op die bevolkingsgroei van die woestynlewende olifante. In die afwesigheid van onwettige jag word voorspel dat die woestynlewende olifantbevolking teen 1997 sal verdubbel tot 'n vlak van 140 olifante.

Alle bewegings van die woestynlewende olifante, insluitende swerftogte van tot 195 km ver, was tot die noordelike Namibgebied beperk. Geen bewyse vir enige bewegings insluitende migrasies na en van die Etosha Nasionale Wildtuin kon gevind word nie. Die hoofkenmerk van die woestynlewende olifante se ruimtelike strategie was hulle opvallende gehegtheid aan hulle tuisgebiede. Die gemiddelde daaglikse afstand wat hierdie olifante beweeg, is 25,7 km. Hierdie beweeglikheid, tesame met die vermoë om tot 96 uur sonder drinkwater klaar te kom, stel die olifante in staat om voedselbronne tot sover weg as 68 km van die naaste waterbron te benut. Die woestynlewende olifante se beweeglikheid, diepgaande kennis van die ligging van natuurlike hulpbronne binne hulle tuisgebiede en vermoë om vir lang periodes sonder water klaar te kom, word as die sleutelfaktore van hulle oorlewing in die woestyn beskou.

Droë rivierlope is die beste beskikbare habitat vir olifante in die noordelike Namib en ook die enigste habitattipe waarop die olifante kan staatmaak vir langtermyn oorlewing. Dit wil voorkom asof vloedvlaktes die olifante se voorkeurhabitat is, terwyl alle ander habitattipes in 'n mindere mate benut word. Die inligting dui daarop dat die huidige getal olifante geen nadelige invloed op die woestynplantegroei het nie. Kontrolering van lugfotos, sowel as die relatiewe ouderdomstruktuur van groot bome in die rivierlope, dui ook daarop dat die olifante vir die laaste 20 jaar geen opvallende nadelige invloed op die boombevolking van die woestyn gehad het nie. Volledige inligting oor die dravermoë van die woestyn is nie beskikbaar nie, maar deur die gebruikmaking van klimatologiese data kan die potensiële dravermoë bereken word in terme van die optimum groot herbivoor biomassa. Hiervolgens is 'n olifantdigtheid van 0,01 per km^2 die maksimum getal olifante wat deur die woestyn onderhou kan word sonder permanente skade aan die plantegroei.

Alhoewel waarskynlik nie geneties verskillend van ander olifante in Afrika nie, maak die woestynlewende olifante optimum gebruik van 'n olifant se natuurlike vermoëns om in die woestyn te kan oorleef. Inligting ingewin gedurende hierdie studie dui daarop dat hierdie olifante goed aangepas is by die woestynomgewing. Verder is hierdie olifante waarskynlik 'n onmisbare skakel in die algemene ekologie van die woestyn, onder andere as gevolg van hulle voedingsmetodes en vermoë om te kan grawe vir water. Die veronderstelde ongeskikte woestynhabitat blyk om huidiglik 'n minimale beperking op die woestynlewende olifantbevolking uit te oefen. Daarom is korttermyn bestuursvoorstelle, vir die bewaring van die woestynlewende olifante, eerder op die vermindering van olifant-mens konflikte, as op habitat verbeterings, gerig. Die bestuursvoorstelle behels die eliminasie van onwettige jag, vermindering van versteurings deur mense, deurlopende beskikbaarheid van watergate, beheer oor voertuigverkeer deur die gebied en die verskuiwing van die veeartsnykundige heining.

Die enigste langtermyn oplossing wat die voortbestaan van die hele woestynekologie egter sal verseker, is die verklaring van die gebied as 'n natuurbewaringsgebied met behoorlike kontrole en bestuur. Die voorgestelde grense van so 'n natuurreservaat is 'n poging tot 'n kompromie tussen die ideale ekologiese eenheid, politieke struikelblokke en sosio-ekonomiese aspekte. Die woestynlewende olifante van die noordelike Namib verteenwoordig 'n unieke ekotipe van _Loxodonta africana_ wat nie alleen van estetiese, wetenskaplike en ekologiese waarde is nie, maar ook 'n potensiele ekonomiese waarde vir die inwoners van die gebied inhou.

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APPENDIX

List of publications and selected reports to date arising from information obtained during the course of the present study.

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