The Roan antelope (Hippotragus equinus, Desmarest 1804), its ecology in the Waterberg Plateau Park

by

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Declaration

I the undersigned hereby declare that the work contained in this thesis is my own original work and has not in its entirety or in part been submitted to any university for a degree.

28 January 1993

Abstract

This study was undertaken in the Waterberg Plateau Park in northern Namibia. Field work took place between January 1988 and September 1989; however relevant information collected since, has been included.

The roan antelope population in the reserve stems from re-introduced animals. A total of 93 were brought in between 1975 and 1981. By 1984 the population peaked at 275 individuals. 186 roan have since been captured and sold.

The main objective of the study was to develop a better understanding of the management requirements for this population of rare antelope.

Approximately one-fifth (32 individuals) of the population was marked with eartags or plastic collars or both. Five animals were radio-collared. This is the first detailed study of roan antelope in such a large study area (40 000 ha), with such a large population and so many marked individuals.

Chapter 3 deals with population dynamics. It is believed that the entire population was accurately counted, aged and sexed. The adult sex ratio was skewed in favour of females, despite the absence of predators large enough to kill adults.

The majority of calves were born during the wet season, from the end of August to March. A positive relationship between early season rainfall and the calf crop in the subsequent year was found. The ratio of juveniles per 100 adult females averaged 41.1 over seven years.

Recorded mortality was too small to identify significant factors.

Two deterministic population models were developed for exploratory simulations and are presented in Chapter 4. Both simulations were fairly successful, giving good correlations with the actual counts.

Nutrition is covered in Chapter 5. Simple nutrient budgets revealed that protein and phosphate requirements were probably not met in the dry season. Calculations based on hand selected forage samples and nutrient requirements of cattle, show that adult roan obtained 15-28% of their crude protein requirements and approximately 10% of the phosphate in the dry season.

The social system of the roan is described in Chapter 6. Four different clans were recognized, each with a distinct home range. The breeding groups in each clan were unstable, splitting up and rejoining at random.

Adult males exhibited territoriality during the breeding season, which is in contrast to most other studies where harem groups were observed. Outside the breeding season, dominant males rejoined bachelor groups or remained solitary.
Home range size and configuration were described using different methods.Home ranges averaged 4800 ha for two clans and the territory size of one male was estimated to be 1200 ha within a much bigger home range. Distinct wet - and dry-season ranges could be distinguished.
Habitat selection is discussed, and was determined primarily by feeding requirements. Forage quality was identified as the major limiting factor and thus the primary determinant of habitat use.
In Chapter 7 management recommendations and research proposals are made to ensure sustainable utilisation, by both live capture and game viewing.

Abstrak

Hierdie studie is in die Waterberg Platopark, in noordelike Namibië, uitgevoër. Veldwerk het tussen Januarie 1988 en September 1989 plaasgevind, maar relevante informasie wat daarna versamel is, is ingesluit.
Die bastergemsbokpopulasie in die reserwe is afstammeling van diere wat hervestig is. 'n Totaal van 93 is tussen 1975 en 1981 ingebring. Teen 1984 het die populasie sy maksimum vlak van 275 bereik. 186 bastergemsbokke is sedertdien gevang en verkoop.
Die hoofdoelwit van die studie was om 'n better begrip van die bestuursbenodighede van hierdie bevolking van 'n skaars boksoort te ontwikkel.
Ongeveer 'n vyfde (32 individue) van die populasie is met oorplaatjies of plastiese nekbande of albei gemerk. Vyf diere is van radionekbande voorsien. Dit is die eerste keer dat 'n gedetaileerde studie van bastergemsbokke gemaak is in so 'n groot studiegebied (40 000 ha), met so 'n groot studiepopulasie en so baie gemerkte diere.
Hoofstuk 3 handel oor populasie dinamika. Dit word aanvaar dat die hele populasie akkuraat getel en volgens ouderdom en geslag ingedeel is. Die volwasse geslagsverhouding was ten gunste van koeie , alhoewel groot roofdiere wat in staat is om volwasse bokke te vang, afwesig is.
Die meerderheid kalwers word in die nat seisoen gebore, vanaf die einde van Augustus tot Maart. 'n Positiewe verhouding is gevind tussen vroeë seisoen reenval en die

kalweroes in die daaropvolgende jaar. Die verhouding van kalwers per 100 volwasse koeie was gemiddeld 41.1 oor sewe jaar.
Die getal dooie diere wat gevind is, was te klein om wesenlike mortaliteitsfaktore te kon identifiseer.
Twee deterministiese populasiemodelle is ontwikkel en word in Hoofstuk 4 voorgestel. Simulasie wat daarmee uitgevoer is, het goeie korrelasies getoon met werklike tellings.
Voeding word in Hoofstuk 5 behandel. Eenvoudige begrotings van voedingsstowwe het getoon dat proteiën- en fosfaatbehoeftes heelwaarskynlik nie altyd gedek word nie. Berekenings gebaseer op grasmonsters wat met die hand versammelde is, en behoeftes van beeste, dui aan dat volwasse bastergemsbokke in die droëseisoen slegs 15-28% van hulle rüproteiën-en 10% van hulle fosfaatbehoefte kan dek.
Die sosiale sisteem van bastergemsbokke word in Hoofstuk 6 beskryf. Vier verskillende stamme (clans) is uitgeken, elkeen met 'n eie tuisgebied. Die teelgroepe in elke stam was onstabiel en het sonder vaste patroon ontbind en weer gevorm.
Volwasse bulle het hulle territorialiteit slegs gedurende die paringstydperk getoon. Dit is in teenstelling met die meeste ander studies waar haremgroepe waargeneem is. Buite die paringstydperk het dominante bulle weer by die vrygeselgroepe aangesluit of alleen gebly.
Verskillende metodes is gebruik om die grootte en konfigurasievan tuisgebiede te beskryf. Die tuisgebiede van twee stamme het gemiddeld 4800 ha beslaan. Die territorium van een bul is op 1200 ha beraam en het binne 'n baie groter tuisgebied gelê. Afsonderlike nat- en droëseisoen tuisgebiede is geidentifiseer.
Habitaatseleksie word hoofsaaklik deur voedingsbehoeftes bepaal. Voerkwaliteit is as die belangrikste beperkende faktor uitgeken en bepaal dus primêr die keuse van habitaat.
In Hoofstuk 7 word bestuurs- en navorsingsvoorstelle gemaak wat gemik is op die volgehoue benutting deur die vangs van lewende diere en besigtiging deur toeriste.

Acknowledgements

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The Ministry of Wildlife, Conservation & Tourism, Namibia, for offering me the opportunity to undertake this study. My thanks go here especially to Dr P.T.van der Walt, previously Head of Research at the start of study, and Dr E.Joubert, current Head of Research, for interest shown in the study.
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My wife Reinhild for her patience and encouragement, while writing up the thesis. My mother especially, kindled an interest for nature in me when I was still a boy and encouraged my research endeavors. I would like to thank my father for his financial help during my undergraduate studies, a foundation needed to tackle this project.
Last, but not least, I want to thank all those many whose names are not mentioned, who helped in one way or another to make a success out of this project. Thank you.

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This dissertation deals with the ecology of the roan antelope *Hippotragus equinus* (Desmarest, 1804) in the Waterberg Plateau Park (hereafter referred to as Waterberg or the plateau), situated in northern Namibia. The main study was undertaken from January 1988 until September 1989, but miscellaneous observations have been collected since and are included where relevant.

1.1. Study area:

The Waterberg Plateau Park is situated in northern Namibia, approximately 80 km east of Otjiwarongo (Figure 1). It is wedge-shaped and the periphery is made of up near vertical cliffs, up to 300m high on the northwestern side. The plateau lies between 1550 and 1850 m above sea level and between 100 to 300 m above the surrounding plains.
It is fenced on the northeastern side, where the plateau gradually runs out into the plain (Figure 2).
The Waterberg is 40 500 ha in extent, of which 40 000 ha is situated on the plateau, to which roan antelope are confined. Approximately 19 000 ha lie in the wilderness area (burning block 6) which is only accessible by foot or on horseback (Figure 4).
The top of the plateau is made up of lithified dunes, known as aeolianite, belonging to the Etjo Formation, which forms part of the Karoo sequence. It is some 200 million years old and at least a 100m thick on the Waterberg. The sandstone is brownish to light grey and medium grained. Windblown Kalahari sand from the Kalahari Basin to the east, covers the sandstone and is up to several meters deep. The Etjo formation overlies the Omingonde Formation, which consists of red to white conglomerate, sandstone and mudstone (Hegenberger 1990). The clay content of the sand on the plateau is relatively low, 93 % of 225 samples have a clay content of less than 20 %. The pH ranges between 3.6 and 6 with a average value of 4.4 for 77 samples analyzed (Jankowitz 1983).

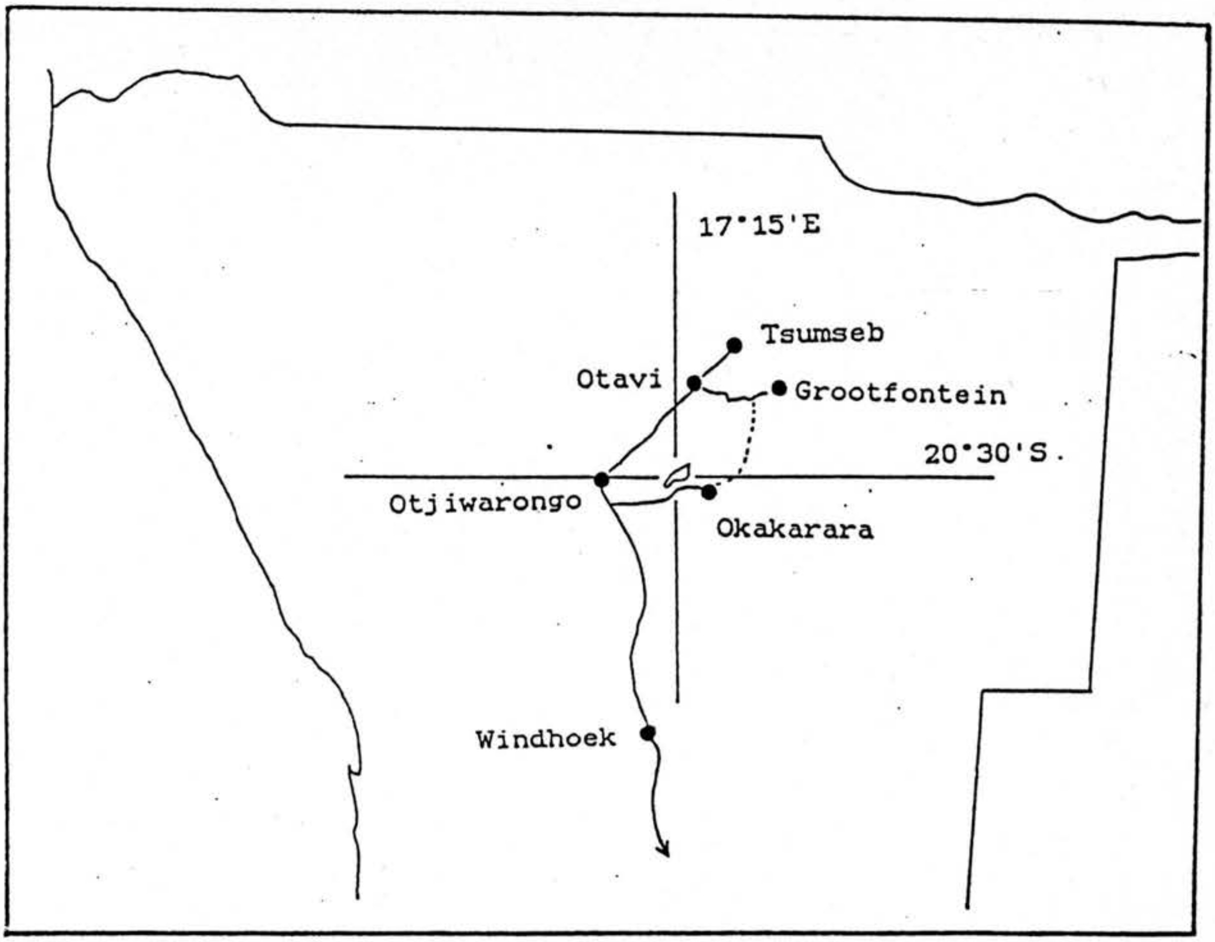
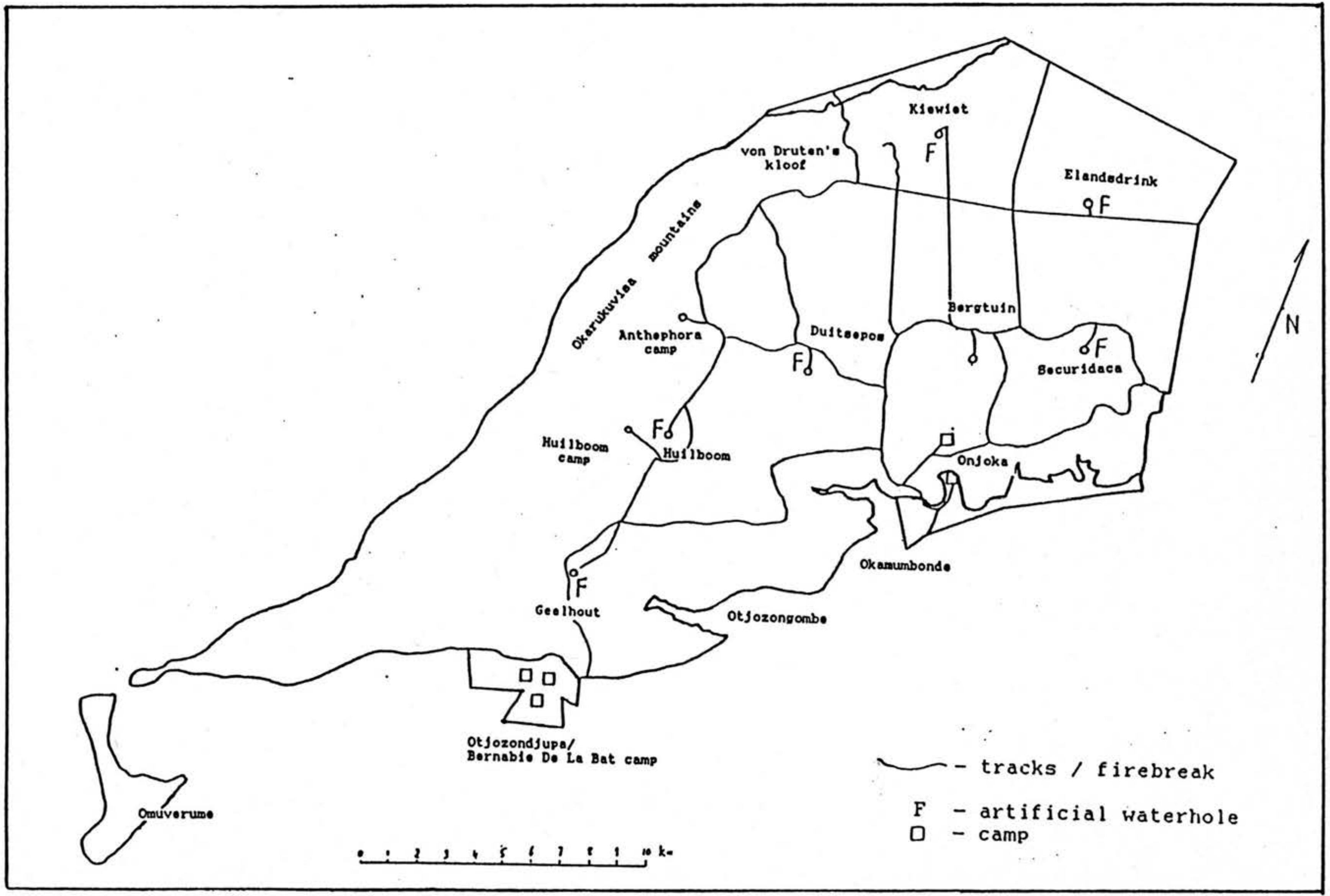


Figure 1: Map of northern Namibia showing location of Waterberg Plateau Park.

Figure 2: Map of the Waterberg Plateau Park.


Kiewiet
F
von Druten's kloof
Elandsdrink
F
Okarukuvisa mountains
Bergtuin
Anthephora camp
Duitsepos
F
F
Securidaca
N
Huilboom camp
F
Huilboom
Onjoka
Okamumbonde
F
Geelhout
Otjozongombe
Otjozondjupa/
Bernabie De La Bat camp
Omuverume
0 1 2 3 4 5 6 7 8 9 10 km
- tracks / firebreak
F - artificial waterhole
□ - camp

The Waterberg Plateau Park falls into the "Hot steppe" climatic zone according to the Köppen system of classification. This means that the mean temperature is above 18°C, the annual average number of days with rain are 40-50 and the deviation of the annual rainfall averages 25-30%. More than 90% of the rainfall occurs from October-March. 4-5 months get more than 50 mm of rain per year. Potential annual evaporation averages 2800-3000 mm. This region is thus rainfall deficient (van der Merwe 1983).
Average annual rainfall measured below the plateau at Onjoka over the last ten years is 450.2 ±75.4 mm. Over the same period the rainfall on the plateau, measured at up to seven gauges, is 354.7 mm. Some of the difference can be attributed to evaporation from the gauges and to damaged gauges. 77% of the rain falls between December and March, with February being the wettest month (Figure 5). No permanent open water is found on the plateau, but water is pumped up to seven drinking troughs.
The larger mammalian species occurring in the reserve are listed in Table 1. Population estimates are based on an annual helicopter census (normally in August), two 48-hour and one 72-hour waterhole count.

1.2. The study population in perspective

a) The status of the Roan antelope in Namibia

Roan naturally occurred only in the northeast of Namibia. Their present status is as follows.
Game Reserves: The only reserve south of the veterinary cordon fence (which restricts the movement of cloven-hoofed animals) containing roan is the Waterberg Plateau Park. It is therefore the only source of breeding stock which is not subject to quarantine regulations. The population is manipulated and stands at 160 animals (Aug.1990) after 77 animals had been caught in 1988. Since 1985 one-hundred-and-eighty-one animals from this population have been made available to other conservation organizations (Transvaal, Natal & Swaziland) and 13 game farmers (in Namibia) for breeding purposes. Each game farmer was supplied with 10 animals, including three or four males. Introductions onto game farms seem to be successful in most cases (pers.com. with farmers). To date anthrax, to which roan are very susceptible, has not been recorded on the Waterberg, but it is present on some of the game farms supplied.

Table 1

Estimated game population sizes on the Plateau 1988 to 1990
(status changes during the period are indicated)

		population sizes
White rhino - *Ceratotherium simum*		30 - 35
Black rhino -*Diceros bicornis*		0 - 25
Giraffe - *Giraffa camelopardalis*		30 - 42
Buffalo - *Syncerus caffer*		44 - 75
Eland - *Taurotragus oryx*		350 - 400
Roan antelope - *Hippotragus equinus*		240 - 150
Sable antelope - *Hippotragus niger*		77 - 90
Gemsbok - *Oryx gazella*		150
Kudu - *Tragelaphus strepsiceros*	appr.	350
Red hartebeest - *Alcelaphus buselaphus*		50 - 75
Wildebeest - *Connochaetes taurinus*		9 - 3
Tsessebe - *Damaliscus lunatus*		16 - 20
Warthog - *Phacochoerus aethiopicus*		350 - 200
Klipspringer - *Oreotragus oreotragus*	appr.	100
Duiker - *Sylvicapra grimmia*	"	100
Steenbok - *Rhaphicerus campestris*	"	200
Brown hyaena - *Hyaena brunnea*	"	10
Leopard - *Panthera pardus*	"	30-50
Cheetah - *Acinonyx jubatus*	"	< 5
Jackal - *Canis mesomelas*	"	50
Caracal - *Felis caracal*		?

Figure 3: Vegetation map of the Waterberg Plateau Park (adapted from Jankowitz 1983).

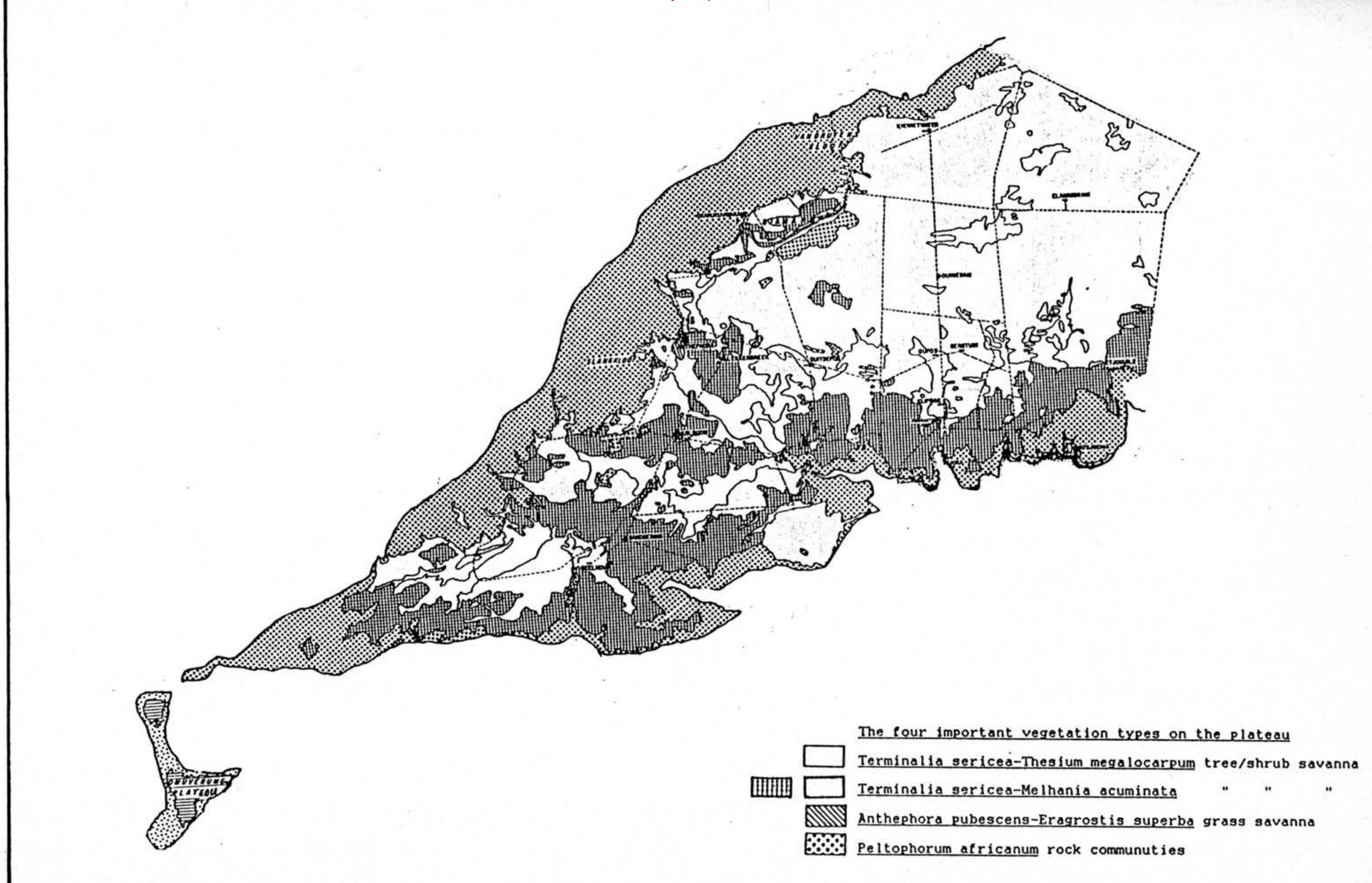
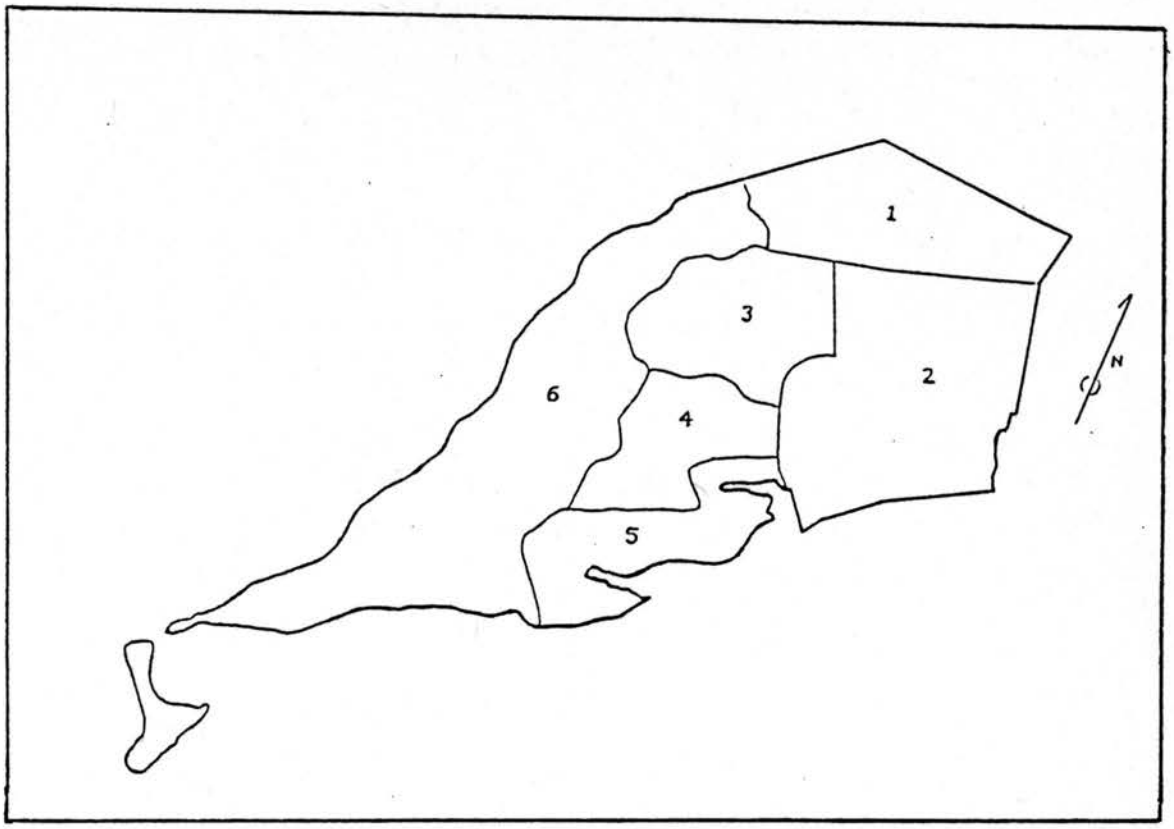

The four important vegetation types on the plateau
Terminalia sericea-Thesium megalocarpum tree/shrub savanna
Terminalia sericea-Melhania acuminata " " "
Anthephora pubescens-Eragrostis superba grass savanna
Peltophorum africanum rock communuties

Figure 4: Map of the Waterberg Plateau Park to show the burning blocks and the Wilderness area (= block 6).

Figure 5: The monthly rainfall distribution for Onjoka from 1980-1990. Monthly averages and extremes are indicated.


1
2
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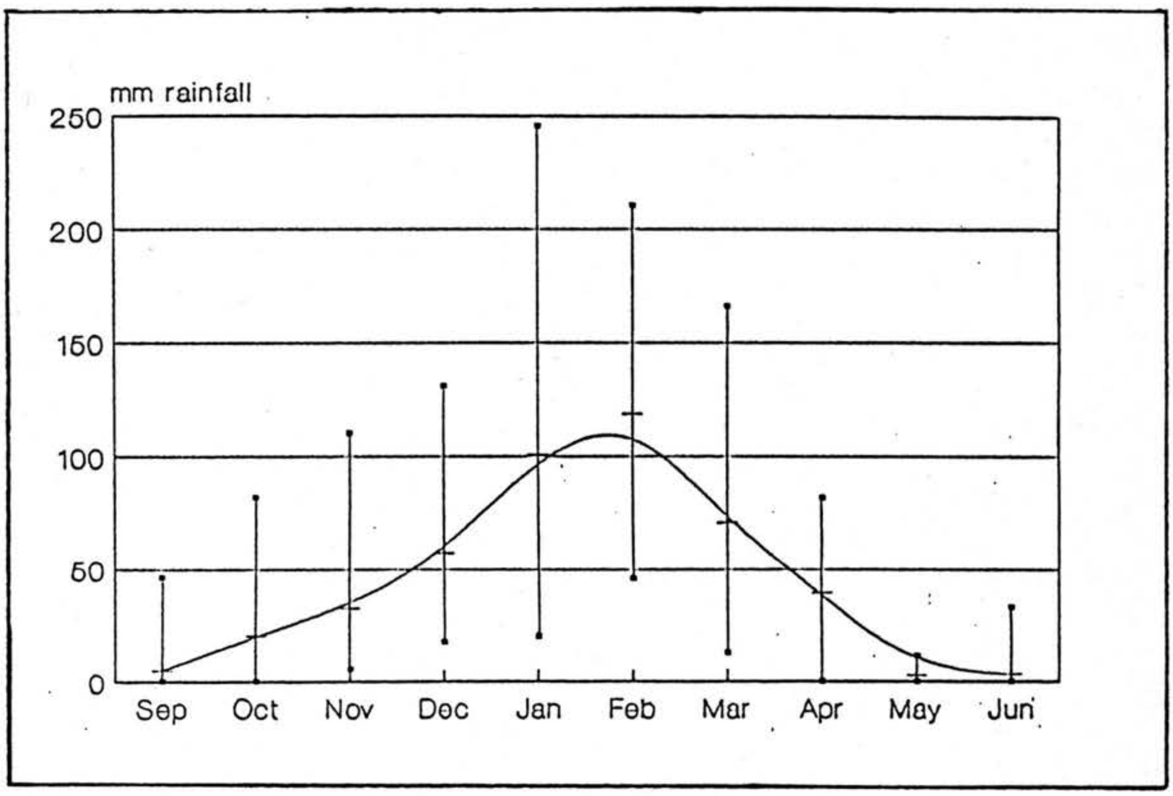
4
5
6
N


mm rainfall
250
200
150
100
50
0
Sep
Oct
Nov
Dec
Jan
Feb
Mar
Apr
May
Jun

51 animals occur in the Etosha National Park (A.Cillier pers.com. 1988), where they are held in the Kaross camp. Anthrax epidemics occur frequently in the rest of this reserve and are thus a potential limiting factor.
In the Mahango Game Reserve in Kavango 24 roan were counted during an aerial survey in 1983 and 43 in 1986. In the Kaudom Game Reserve (470 000 ha) a larger population occurs, probably numbering a few hundred animals. An estimated total for the whole Kavango, including the two reserves, is 1000 animals (C.Grobler pers.com. 1988).
Communal and commercial farming area: In Bushmanland the roan population is decreasing and numbers approximately 50 animals (M.Loots pers.com. 1988).
Both in the western and eastern Caprivi roan appear to be very rare, the population seems to be decreasing.
A few animals still occur naturally on private farms, mainly cattle ranches, in the Grootfontein and Otavi districts.
Van der Walt (1989) estimates the roan population for the whole of Namibia to be just over a 1000 animals.

b) Study population

In September/October 1970, seventy-four roan were introduced into the Koabendes paddock (765 ha) at Otjovasandu, Etosha National Park. They had been caught in the Kaudum Omuramba in the Kavango. Four died within 2 days and 27 calves were born in the next 3 months.
The animals were then given access to the 14 300 ha Kaross camp. Groups comprising 4-12 animals were observed, each with a bull, females and calves. In addition, two large breeding herds formed, each numbering up to 30 animals. Solitary bulls were also seen.
Helicopter censuses carried out in September 1972 and August 1973 produced totals of 107 and 159 respectively.
Calves were born throughout the year. One calf was killed by a leopard.
Introductions of the Kaross roan to the Waterberg Plateau Park, comprised 70 in 1975, 7 in 1976 and 16 in 1981 (Hofmeyr 1973 & 1974). Sex and age ratios of the animals introduced are not known.

1.3. Previous studies

Joubert (1971, 1974b and 1976) conducted studies on the roan antelope's social behaviour and population ecology in the Kruger National Park. He concentrated on a group of animals in a one square mile enclosure.

Wilson (1975) investigated limiting factors to both roan and sable antelope in Transvaal nature reserves.
Ben-Shahar (1986) carried out a study on roan, sable and tsessebe in the Waterberg, Transvaal.
Mr I.M.A.Heitkönig is presently engaged in a study on the feeding behaviour of the roan in the Nylsvley Nature Reserve.
Apart from some of Joubert's observations, the study areas used by these researchers, were less than 2500 ha in extent. No detailed studies have been undertaken in optimum roan habitat.
Various short investigations regarding roan ecology were undertaken inter alia by Oboussier (1963) in Angola, Best et.al (1970) and Child & Wilson (1964) in Zimbabwe, Sekulic (1976, 1978a & 1978b) and Allsop (1979) in Kenya, Backhaus (1959) in Zaire, Stark (1986a & 1986b) in Cameroon and Poché (1974) in West Africa.

1.4. Vegetation studies on the Waterberg

Two Ph.D. studies on the vegetation of the plateau have been undertaken. Rutherford (1975) worked on the Omuverume plateau, which is separated from the main plateau by cliffs and is inaccessible to game. He concentrated on vegetation structure, productivity and phenology.
Jankowitz (1983) and Jankowitz & Venter (1987) described and mapped the vegetation communities on the main plateau. In his vegetation map for the reserve he recognizes four major plant communities (Figure 3). Common trees are *Acacia ataxacantha*, *Burkea africana*, *Combretum collinum*, *C. psidioides*, *Dichrostachys cinerea*, *Grewia flavescens* and *G.retinervis*, *Lonchocarpus nelsii*, *Ochna pulchra*, *Peltophorum africanum*, *Terminalia sericea* and *Ziziphus mucronata*.
Common grass species include: *Brachiaria nigropedata*, *Andropogon schirensis*, *Digitaria seriata*, *Eragrostis pallens*, *E.rigidior*, *E.jeffreysii* and *Panicum kalaharense*.
For detailed vegetation descriptions see Jankowitz & Venter (1987) and Rutherford (1975).
The plateau is divided into 6 burning blocks, each of which is burnt every 6-8 years (Figure 4).

Chapter 2: Description of the study

In this chapter the motivation for the present study is explained and relevant literature is reviewed. The approach and the methods used are then described.

2.1 Motivation for the present study

The Waterberg Plateau Park was established in 1972. One of its main functions is to serve as a breeding area for rare game. Roan antelope were first resettled on the plateau in 1975, as part of the re-introduction program. The species had become locally extinct early this century, as a result of over-hunting (Mossolow 1976). Further introductions followed and by 1981, 93 roan had been released on the Waterberg. The population increased to approximately 275 in 1984. In 1985 the first 72 roan were captured, followed by a further 114 in total in 1987 and 1988.
The roan antelope is either threatened with extinction or rare in all southern African countries (Fuggle & Rabie 1983). It is a magnificent animal and this, together with its rarity, makes it economically very valuable. The demand for breeding stock, from both nature conservation bodies and game farmers, is high.
A sound scientific basis was thus required to plan the management of the Waterberg population. Accordingly an intensive short-term (20 months) study was initiated to answer a series of key questions, posed by the then Department of Nature Conservation in Namibia:

a) What factors, if any, are limiting to roan on the Waterberg ?

b) Do limiting factors exist that can be overcome by management ?

c) Can the population be used as a regular source of supply to other conservation areas?

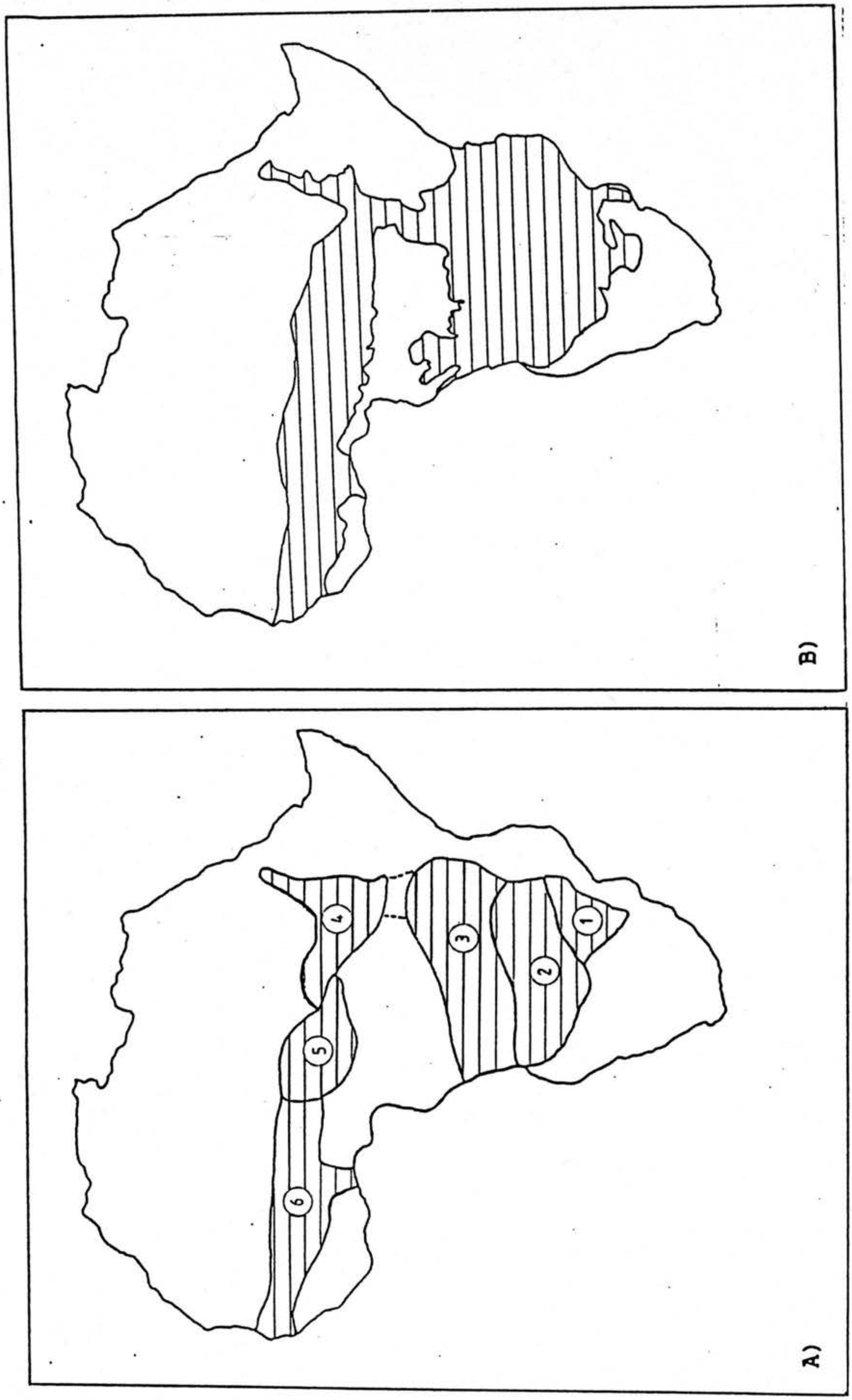
2.2 Summary literature review

Taxonomic status: Roan antelope, together with the sable antelope (H.niger) and the extinct bluebuck (H.leucophaeus) form the genus Hippotragus which, with Oryx and Addax, belong to the tribe Hippotragini of the family Bovidae.
Ansell (1972) lists 6 subspecies of roan antelope in Africa one of which, H.e.cottoni, occurs in Namibia (Figure 6).

Distribution in Africa: Roan antelope are distributed from West Africa, where they attain relatively high densities, to Eastern, Central and Southern Africa (Figure 6a).
In Namibia the Waterberg (Figure 7a) lies on the edge of the historical distribution range (Shortridge 1934, Bigalke 1958, Gaerdes 1967, Joubert & Mostert 1975 and Joubert 1976). The distribution of the roan antelope corresponds well with that of a typical tropical savanna tree, Burkea africana, as shown in Figures 6b and 7b.
Densities of roan in different areas are given in Table 2.
Morphology: Roan antelope are the third heaviest member of the family Bovidae, only eland and buffalo are bigger. Males attain an average mass of 250-300 kg, females are 50 kg lighter. Roan have shorter backward curved horns than sable. The average length for males is 50-75 cm and the African Rowland Ward record is 99.1 cm. Roan are morphologically adapted to grazing in medium to tall grass swards. The low angle of incisor insertion is that of a typical grazer. Roan have a narrow muzzle with which they can select particular clusters of leaves from taller grass swards, as opposed to a broad muzzle which is more effective in maintaining an adequate rate of intake from short grass swards (Owen-Smith 1982, 1985, Novellie 1990).
Feeding behaviour: Roan antelope are predominantly grazers, utilizing mainly medium to tall perennial grasses, such as Themeda triandra, Hetropogon contortus and Schmidtia pappophoroides. Browse is utilized at the end of the dry season, species taken include Acacia spp., Grewia spp., Capparis tomentosa and Lonchocarpus capassa (Child & Wilson 1964, Poché 1974, Wilson 1975, Joubert 1976, Geerling 1979).
Social behaviour: Roan antelope are gregarious animals with breeding herds usually numbering 10 to 20 individuals. The breeding group can be a proper harem herd, in this case a specific male being associated with a particular female group throughout the year, as is the case in the Kruger National Park. On the other hand a group of females with their offspring may move through several male territories. This has been observed in Angola (Joubert 1976, Wilson 1975, Oboussier 1963). Breeding group home ranges extend over an area of 6 000 to 10 000 ha.
Males reaching 2-3 years of age, are forced out of the herd and either become solitary or form bachelor groups. Social hierarchies are well developed in both sexes. Breeding groups are usually led by the dominant female.
Reproduction: Females reach sexual maturity at two years of age and have their first calf when three years old. The

Figure 6: A) The distribution of the roan antelope in Africa (based on Joubert 1976, Skinner 1990). B) The distribution of a typical savanna tree, *Burkea africana*, in Africa (adapted from Rutherford 1982).

Legend:
1. *Hippotragus equinus equinus*
2. *H.e. cottoni*
3. *H.e. langheldi*
4. *H.e. bakeri*
5. *H.e. sharicus*
6. *H.e. koba*


B)
A)
1
2
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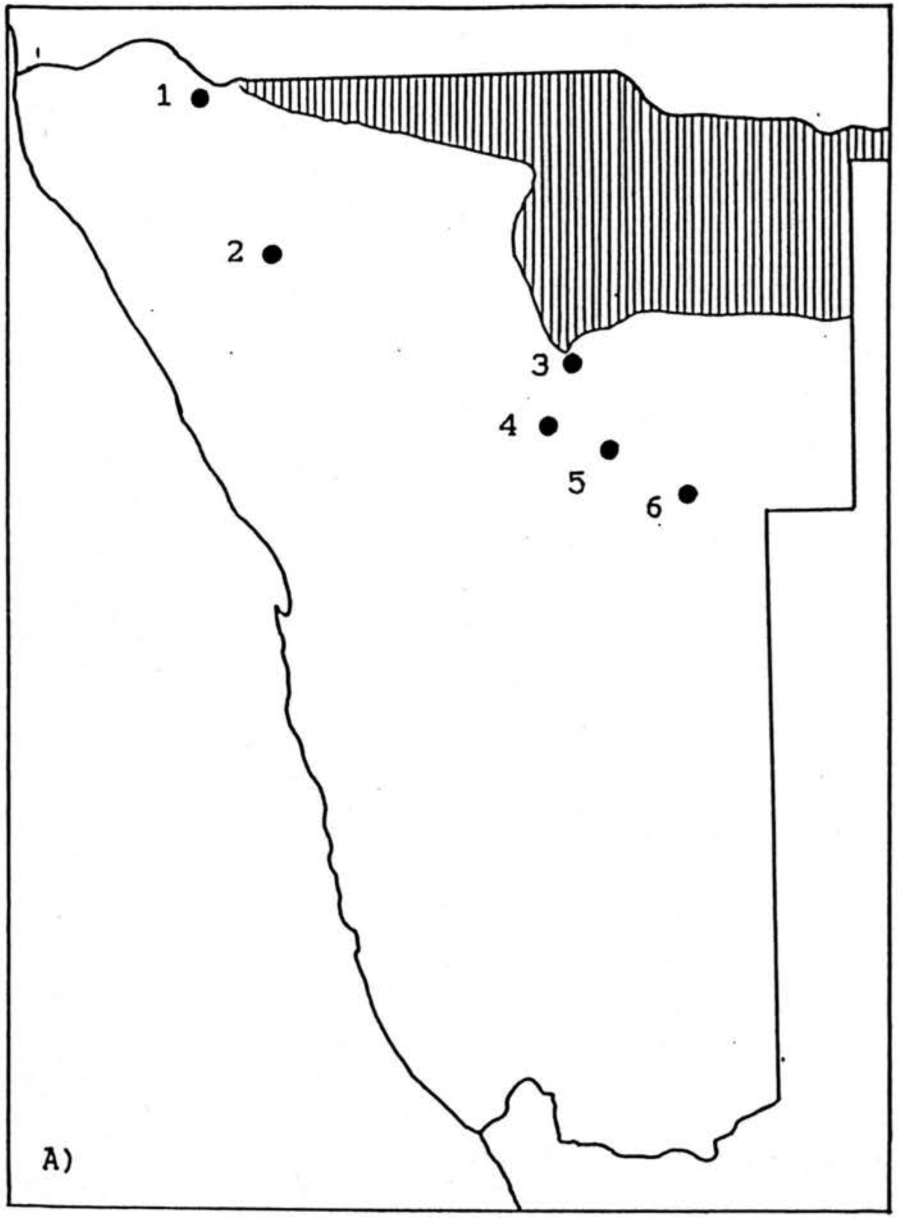
6

Figure 7: A) The distribution of the roan antelope in Namibia, shaded area represents distribution area as recorded by Shortridge (1934). B) The distribution of a typical savanna tree, Burkea africana, in Namibia (adapted from Leser 1982).

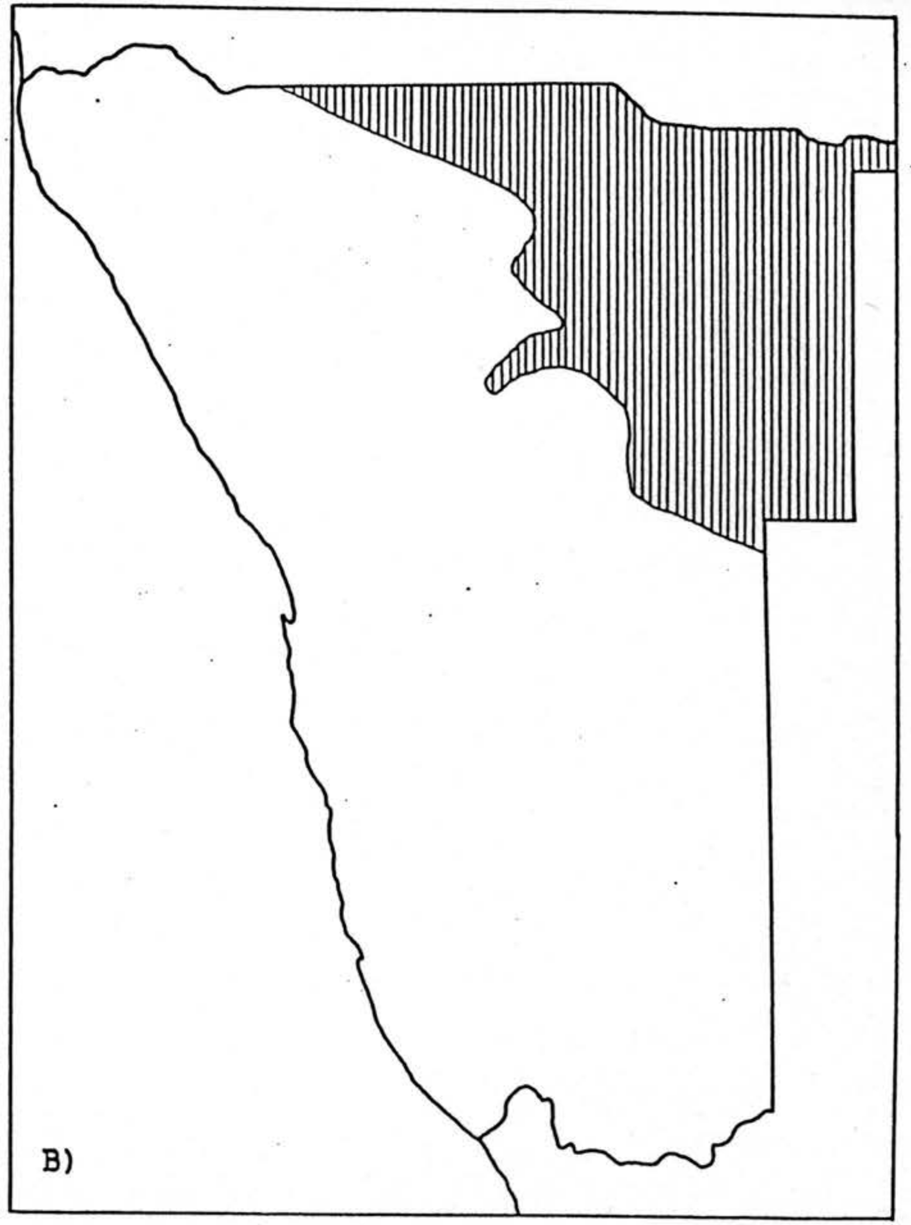
Legend: 2. Otjovasandu (introduced population)

Historical distribution localities (Gaerdes 1967)

1. West of the Ehombo mountains
3. Waterberg Plateau Park
4. Farm Osire
5. " Kalidona
6. " Anderson



A)



B)

Table 2

Roan densities in African conservation areas

Reserve	Country	Area (km²)	Rainfall (mm)	density (/km²)	Author
Percy Fyfe	South Africa	4.3	421	6.98	Wilson 1975
" "		21	421	2.57	" "
Bouba Ndjida	Cameroon	1800	1200	2.42	van Lavieren & Bosch 1977[3]
Deux Bale	Upper Volta	566	970	2.12	Sihvonen 1974[3]
Bouba Ndjida	Cameroon	2200	1200	1.98	van Lavieren & Esser 1979
Arli	Upper Volta	1000	1000	1.90	Green 1981[3]
Pendjari	Benin	2740	1050	1.83	Sayer[1]
Fina	Mali	2250	1000	1.75	Sayer[1]
Po	Upper Volta	468	900	1.66	Heisterberg 1975[3]
Lambe Valley	Kenya	70	--	1.5	Allsopp 1979
Kainji	Nigeria	3924	1100	1.50	Milligan 1981[3]
W	Niger	3000	730	0.95	Poché 1975
Kaross	Namibia	143	300	1.1	see sec. 1.3b
Waterberg	Namibia	400	450	0.88 -0.38[2]	Erb (this study)
Saint-Floris	C.A.R.	1007	1150	0.50	Spinage 1976[3]
Yankari	Nigeria	2250	1000	0.16	Henshaw 1975
Comoé	Ivory Coast	12500	1200	0.08	Geerling & Bokdam 1973

[1] cited as pers.com. in Milligan et al. (1982)
[2] for population sizes ranging between 350 to 150 roan
[3] cited in Milligan et al. (1982)

gestation period is nine months and, partly due to a post partum oestrus, females are capable of having six calves in five years (Joubert 1976). Roan have poorly defined calving seasons in Central and East Africa (Ansell 1960, Blower 1961, Child & Wilson 1964, Smithers 1966, Fairall 1968 and Joubert 1971, 1976). The mother-calf relationship is very loose, during the first four to six weeks the calves lie out and later form nursery groups.

Joubert (1976) recorded a high initial mortality among small calves. The mortality rate for young males increased, as they got evicted from the breeding group at about two years old. Adult males experience a higher mortality rate than females. In a small sample, predation accounted for 2.6 males for every one female. However roan are an unimportant prey species in the Kruger N.P.. No mortalities due to intra-specific fighting were recorded by Joubert (1976), not even in the 256 ha enclosure with more than two adult males present. Wilson (1975) recorded the killing of a adult male by another one in a 430 ha camp and a yearling heifer in a 2061 ha camp, both on Percy Fyfe Nature Reserve. Roan calves are susceptible to cytauxzoonosis and babesiosis. Adults are susceptible to anthrax and are also threatened by Rinderpest (Stewart 1964, Wilson et al. 1974 and Joubert 1976).

Roan antelope attain an age of 12-14 years in the wild (Joubert 1976).

2.3 Material and methods

This was the first formal study undertaken on one of the game species on the Waterberg. It was thus difficult to anticipate what to expect. The approach had to be very broadly based to detect possible limiting factors as well as differences between different segments of the population. The study design had to be modified as unexpected difficulties or opportunities arose (Table 3).

The study took place towards the end of a dry climatic cycle. In Figure 8 the annual rainfall for the farm Okosongomingo, adjacent to the Waterberg, is shown. The long term (1914-1990) average rainfall is 470 ±183 mm per year. During the last dry cycle (1980-1990), the average dropped to 382.5 mm.

Fairly early in the study it was realized that visibility of the animals was limited. Finding particular individuals regularly would be difficult, but very important. Five adults, one male and four females, were thus radio-collared with Telonics transmitters, emitting an FM signal in the

Table 3
A summary of results obtained from counts, the timing of captures and how the study fits into this time period.

1984

March aerial census — 111 roan
Waterhole count — 378 roan

1985

March capture — 72 roan
August aerial census — 140 roan
Waterhole count — 248 roan

1986

August aerial census — 178 roan
Waterhole count — 329 roan

1987

July aerial census — 144 roan
July capture — 37 roan
Waterhole count — 275 roan

marking of 20 roan in October with eartags/plastic collars

1988

Start with field work in January

Radio-collaring of 3 females in March

June waterhole count — 192 roan
July aerial census — 215 roan
July capture — 77 roan

Tagging of 10 roan in August
Radio-collaring of 2 roan in August

August waterhole count — 156 roan

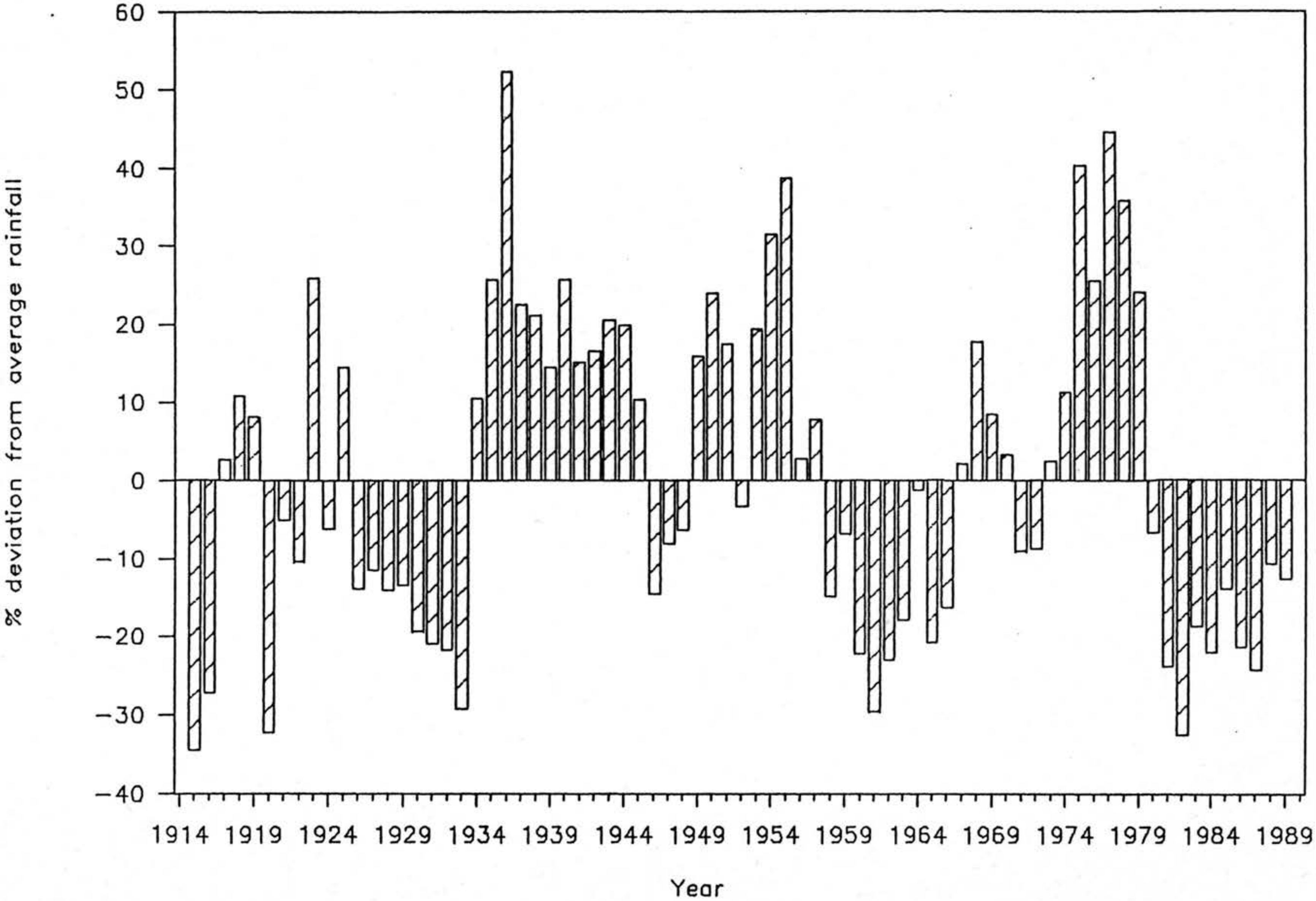
1989

Remove the 3 radio-collars, that are still working, in June

August waterhole count — 150 roan

End of intensive field study period in September

Figure 8: Rainfall on the farm Okosongomingo for 1913/14 to 1989/90. The three year running average percentage deviation from the mean rainfall (470 mm) is indicated.


60
50
40
30
20
10
0
−10
−20
−30
−40
% deviation from average rainfall
1914 1919 1924 1929 1934 1939 1944 1949 1954 1959 1964 1969 1974 1979 1984 1989
Year

148–150 MHz range. A further 29 roan were marked with eartags (Lone Star cattle tags), including 13 adults which were also marked with plastic Stercolite collars. Eartags have been successfully used elsewhere, for example to mark mule and white-tailed deer in the United States and reedbuck in South Africa (Beasom & Burd 1983, Howard 1986). Of the 29 roan, two adult males, marked in October 1987, were never resighted and have been excluded from all calculations. Two tagged males caught during the July 1988 capture were also excluded from the calculations.

Several roan, especially adult males, could be identified from natural markings, such as horn deformities, torn eartips and scars. Notes were kept on such abnormalities to identify these individuals.

Due to the size of the study area and the relatively low roan density, most observations were made from a vehicle while searching for roan in likely habitats. Some were also made from horseback, especially in the wilderness area. Animals visiting waterholes during the dry season were classified by age and physical condition.

The age class criteria of Joubert (1976) were used (Table 4).

Animals observed in the field were aged and sexed where possible, especially if in a recognizable group.

Roan had a flight distance of between 20 and more than 200m. This depended on the individual as well as on previous exposure to disturbances, such as a capture operation. This shyness together with limited visibility, precluded extended observations on individual animals.

Blood samples were collected opportunistically from captured animals. Liver samples were taken from two old males which were destroyed. All chemical analyses were performed by the Windhoek Agricultural Laboratory following the methods as described by Grant (1989).

Standard body measurements were taken from all captured roan and horns of animals found dead were measured.

Table 4

Age classes for roan antelope based on Joubert (1976)

1 = 0-2 months horns not visible yet
NEWBORN

2a = 2-6 months horns shorter than 8 cm, no ridges
JUVENILE 1

2b = 7-12 months horns between 8-19 cm and with a maximum of 2 ridges
JUVENILE 2

3 = 12-24 months 2-9 ridges on the horns, still straight
SUB-ADULT 1

4 = 24-36 months 9-17 ridges and are curved, although not complete
SUB-ADULT 2

5 = 3-5 years 17+ ridges, horns with full backward curvature. Rings at the base follow tightly on one another. They can form a smooth base up to 3cm long.
YOUNG ADULT

6 = 6-10 years horn shape as above but with a smooth basal area 4-10 cm long.
ADULT IN FULL PRIME

7 = 10+ years old basal area of horns smooth surfaced for more than 10 cm, horns appear worn.
OLD ADULT

Chapter 3: Population dynamics

3.1. Introduction: One of the most important and basic objectives of this study was to determine the size and its age and sex composition. Different counting techniques were used the results were compared and a best estimate was chosen. Choice of the best estimate was based on the assumption that the counts, following an approximate trend, with regard to population size, especially for waterhole counts, are more representative of the true population size than the exceptional count.
Age and sex composition determined during the annual waterhole counts (total count) was assumed to be representative of the population. This data was then used to evaluate the demographic vigour of the population, i.e. how it reacts to the collective action of all the environmental variables affecting it. Vigour should indicate the extent to which the population is limited by its environment. The assessment was facilitated by the fact that the study population is geographically closed.

3.2. Methods:

3.2.1. Population estimates - Aerial censuses: Annual helicopter censuses, covering the entire plateau, were undertaken from 1984 to 1988. Prior to 1984 censuses, some of them from a fixed-wing plane, did not cover the entire plateau systematically (Cooper 1988 pers.com.).
The same senior official was involved as one of the counters in all the 1984 -1988 counts, and although the actual flight path was adapted over the years, the method as such was the same. The timing of the census, an important factor (Figure 10) in a largely deciduous woodland savanna, could not be standardized.

The count takes approximately 14 hours to complete and is spread over two days. Another ½ day is used to count the separate Omuverume plateau and the area below the mountain, both without roan. The plateau is divided into 25 blocks which are counted in a particular sequence. The game is counted by two observers, assisted by the navigator and pilot. Strips are flown 500m apart, with the exception of some specific blocks along the rocky periphery, where they are 300m apart. Ageing and sexing of individuals in groups is difficult and was done only partially. Identification of tagged individuals proved impractical so that no data was generated for mark-recapture population estimates.

Waterhole counts: These are undertaken annually in the dry season at the seven artificial watertroughs, where all the game has to drink. Usually two 48 hour count is undertaken, one each in June and July, and one 72 hour count in August. Rangers and labourers, equipped with binoculars, operate as two man teams, each responsible for counting at a particular waterhole. Counters operate from permanent hides to which the game is accustomed, placed approximately 50 meters from the water. Standard data sheet are used and repeated drinking by the same individual is noted when recognized. Game is aged and sexed as far as possible. In the case of roan, Joubert's (1976) aging criteria in a simplified form are used. Animals less than a year old are regarded as juveniles, subadults include yearlings and two year-olds and individuals three years and older are regarded as adults.

Counts were added up immediately after being completed, in the presence of the senior observer from each waterhole.

3.2.2. Recruitment through natality: Young calves were aged as accurately as possible during field observations and based on this, the date of birth was estimated for as many different calves as possible for a particular year. The calves in the different breeding herds were counted where possible, especially during the waterhole counts.

3.2.3. Mortality: Prior to the study only six roan antelope deaths had been recorded on the plateau, too few to make any deductions about possible mortality factors. Mortality rates during the study period, October 1987 to August 1991, are estimates based on the survival of marked animals and on actual mortalities recorded. Once marked a particular individual was allocated to a sex/age group and monthly records were kept using a table similar to Table 9. Subadults which became adults (males at 5 years, females at 3 years) during the study period were transferred to the adult age class. The number of roan-years were counted for each sex/age class. If a mortality occurred in a particular sex/age class, the number of months that the animal would have remained in this category during the study period, if it had not died, were added. If an individual disappeared, death was assumed to have occurred directly after the last sighting. This approach gives a somewhat higher mortality rate, since not all animals die directly after being last seen. The average annual mortality rate estimate was calculated as follows:

$$\text{mortality rate (\%)} = \frac{\text{recorded mortalities by } sex_j/age_i}{\text{roan-years by } sex_j/age_i} \times 100$$

3.3. Results:

3.3.1. Population estimates

The following manipulations have to be taken into consideration when making population estimates.

Re-introductions - Only total numbers of roan introduced could be obtained. The age and sex ratios allocated in Table 5 are based on the population model (see Chapter 4).

Captures - The ages and sexes of roan captured were recorded and are given in Table 6.

August was chosen as the month to compare population sizes between years, when the last waterhole count has been completed, capture operations are over and before the next calving season starts.

Aerial census: Only one aerial census was undertaken during the study, namely in July 1988 just before the capture operation. It was considered to be successful, 215 roan were counted out of an estimated population of 240 (156 roan plus 80 removed or in the boma).

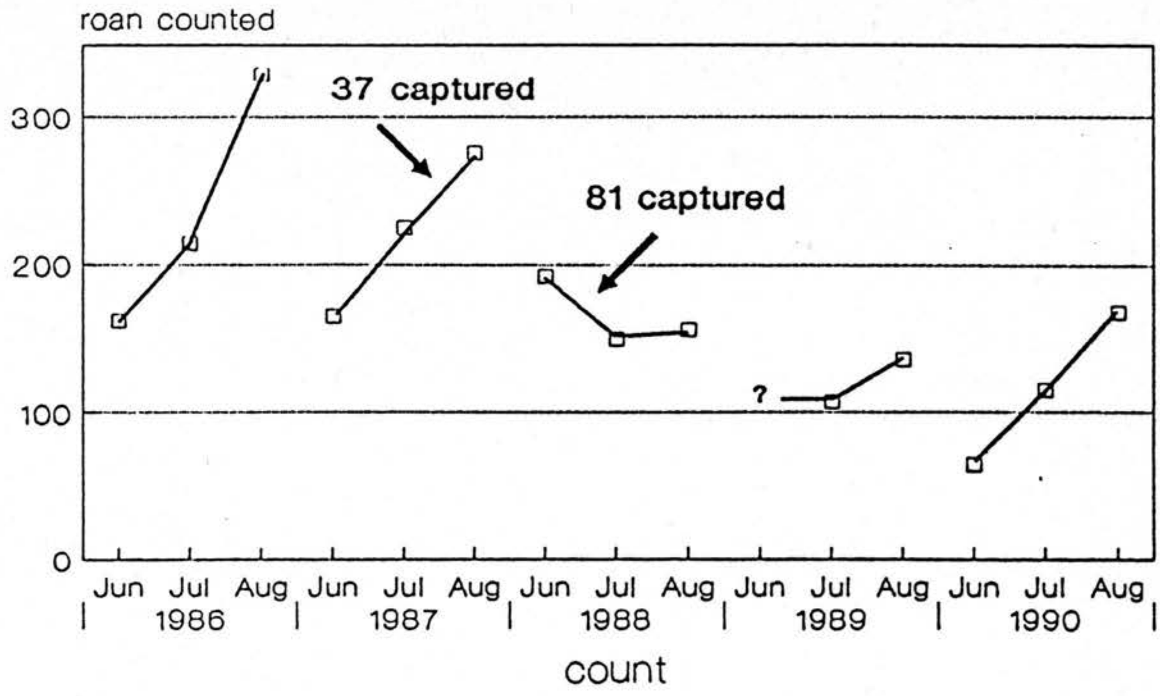
Census figures are given in Table 7 and represent the actual number of different animals counted.

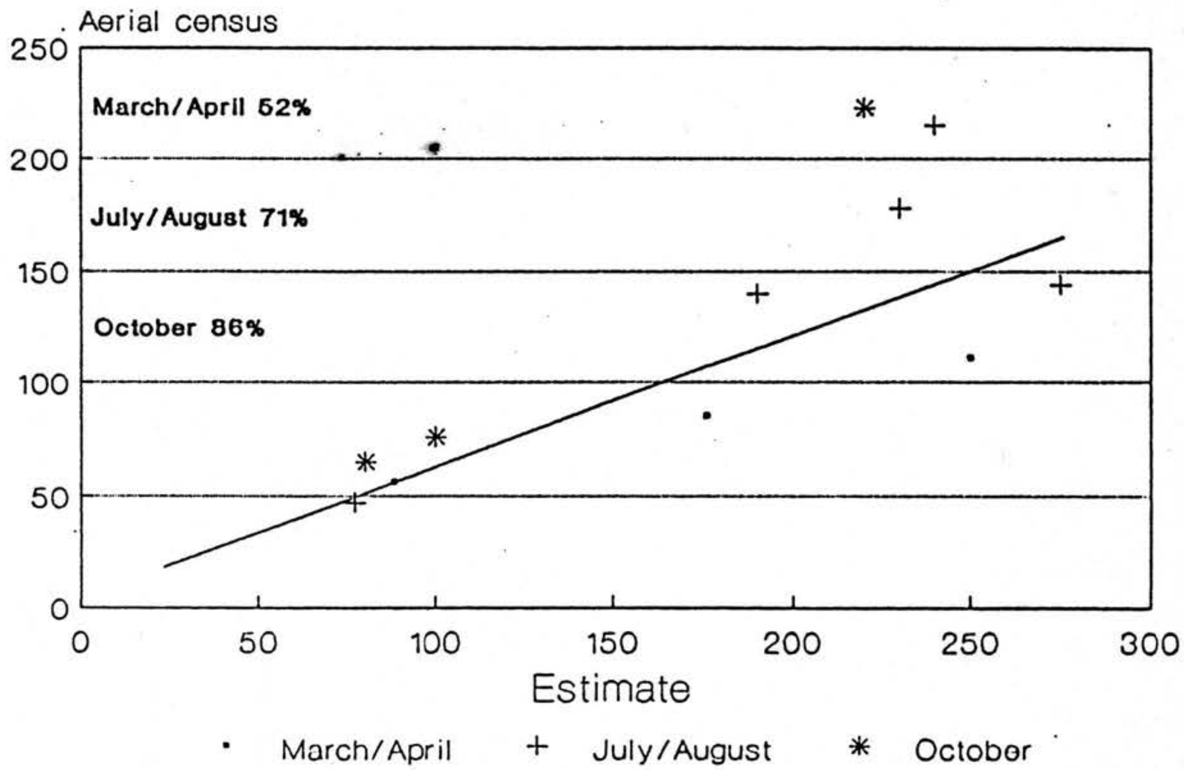
Waterhole counts: - Population estimates based on August waterhole counts are given in Table 8. A comparison between the three waterhole counts each year for the period 1986 - 1990, is presented in Figure 9.In 1988 I counted once at each of the three important waterholes Huilboom, Geelhout and Duitsepos, during the routine waterhole counts.

For the 72 hour waterhole count in August 1988, there were 30 marked animals in the population. They had been marked previously and were either seen during the count or afterwards. Two adult males and a subadult male and female were not observed during the count (Table 9).

Figure 9: Waterhole count figures for roan antelope, 1986 - 1990.

Figure 10: A comparison between aerial census counts and the best estimate, taking timing of helicopter census into consideration.


roan counted
37 captured
81 captured
?
300
200
100
0
Jun Jul Aug Jun Jul Aug Jun Jul Aug Jun Jul Aug Jun Jul Aug
1986 1987 1988 1989 1990
count


Aerial census
March/April 52%
July/August 71%
October 86%
250
200
150
100
50
0
0 50 100 150 200 250 300
Estimate
March/April
July/August
October

The 30 marked animals were seen on average 1.6 times each during the August 1988 count, compared to 1.7 times for all the roan considered to be different individuals.
The 1989 waterhole count proved to be very unsatisfactory. Only 136 out of at least 148 roan were observed. Of the 24 tagged animals known to be in the population, only 54% were counted.
The 1990 August count gave a population estimate of 160 animals. 18 marked roan drank on average 1.6 times during the 72 hour count. Other identifiable individuals were estimated to have visited the water 1.8 times.
The best estimates of population size in the different years were derived by taking all counts in a particular year and differences between consecutive years into consideration. Expectionally high or low counts within a year were ignored. Clearly annual growth rates of 80, 39 and 52 percent in consecutive years are impossible (Table 10). In these cases the original waterhole count sheets were re-examined and corrected for undercounts of animals drinking more than once (see also Sec. 3.4.1. p.30). Best estimates of totals and age and sex compositions are given in Table 11 and Figure 11.

3.3.2. Recruitment

Calving season: The first new born calf of 1988 was seen in the field at the end of August. At the same time a calf was born in the boma to a female caught in July. By the end of September another two calves had been observed, while by the end of October each group had one or two small calves. The bulk of the calves, however were born from October to March. This pattern was repeated during 1989. Very little calving was observed between April and late July. A female calving for the first time, when four years old, had her calf in June/July.

Calving/weaning success: The average ratio of juveniles to 100 adult females observed over seven years was 41.1 (Table 12), with a range of 31.6 to 49.4. Since these figures were obtained during the August waterhole counts, when calves were already approximately eight months old, they do not include post natal mortalities. A relationship between rainfall during the early calving season (September-December) and the observed calf to adult female ratio during the next August waterhole count was observed. The regression equation $y = 0.0855x + 30.6$ ($r=0.819$) describes this relationship, where y is the percentage of adult females

Table 5

Summary of roan introductions 1975 - 1981 (see text)

	Total	Adults		Subadults	
		Male	Female	Male	Female
1975	70	10	40	5	15
1976	7	2	5		
1981	16	4	6	2	4
Total	93	16	51	7	19

Table 6

Summary of roan captures 1985 - 1988

		Juveniles		Subadults		Adults	
		Male	Female	Male	Female	Male	Female
1985 Relocated			4	10	19	12	25
Capture mortality				1			1
Total	72		4	11	19	12	26
1987 Relocated				6	2	7	20
Capture mortality						1	1
Total	37			6	2	8	21
1988 Relocated			1	8	10	23	37
Capture mortality							2
Released*					1	2	1
Total	77		1	8	9	21	38
Total	186		5	25	30	41	85

* plus one calf born in the boma

Table 7

Aerial census results

Year	Month	Roan counted	Notes
1976	August	47	
1977	October	65	
1979	April	56	
1980	October	76	
1982	April	85	
1983	October	223	
1984	March	111	
1985	August	140	72 captured in March
1986	August	178	
1987	July	144	before the capture of 37 roan
1988	July	215	" " " " 77 "

Table 8

Waterhole counts (August estimates)

Year	1982	1983	1984	1985	1986	1987	1988	1989	1990
Roan	166	234	378	248	329	275	156	136	168

during August with a calf and x is the previous seasons rainfall (in mm) until the end of December.
During this study it proved to be impossible, to estimate fecundity and early post natal survival rates separately.

3.3.3. Mortality

A summary of causes of mortality recorded for roan on the plateau is given in Table 13. For 42% the cause of death is unknown; in most cases the carcasses were several weeks old when found. Two calves and a yearling were killed by leopards and one calf was killed by a cheetah. The two roan that died on a neighbours farm had escaped from the plateau. The adult male became entangled in a cattle fence. Two adult males too weak to walk properly, were destroyed. Both had no enamel left on the crowns of the maxillary molar I teeth.
Parasites collected included Setaria labiatopapillosa in mesenteric membranes of four animals sampled, and a Stilesia sp in the liver of one male. Thysaniezia giardi was also identified. Bloodsmears proved negative for blood parasites.
During the study period two adult cows in poor condition were observed with a heavy tick load around the anal area. In both cases the ticks were visible with binoculars at 20-30m.
No roan mortalities due to disease have been recorded on the Waterberg to date.
During 1989 the carcasses of 6 males were found. One was a young (4½ years old) ear-tagged animal and two were very old with worn down teeth. Taking an average 1989 adult male population of forty individuals, these six observed mortalities would represent a 15% mortality rate for that year. It is however unlikely that all mortalities were recorded.
In Table 14 the estimated mortality rates, based on the survival of marked animals, are given.

Table 9
Resightings of marked roan during the June, July and August waterhole counts

```
                             1988    1989¹   1990     1991
Adult bull             1     +-+----------
    (7)                2
                       3
                       4     +---+-----+-+------+-----+---+
                       5
                       6     +---+
                       7
                       8     -----------------------------+
                      29         +-----+----------------+-+
                      30         +-----+----+
                      31         +---------

Subadult              17     --+---------+
    (5)               18     +---+
                      19     ----+
                      20     --+-+-------+------+-----+-+-+
                      24       +-+-----+-+------+-----+---+

Adult cow              9     --+-+-----+-+------+-----+---+
    (13)              10     +-+-+-----+--------+-----+---+
                      11     +-+-+--------------+-----+-+-+
                      12     +---+-----+-+------+-----+---+
                      13     +---+-------+--+---+-----+---+
                      21     --+-+--------------+-----+
                      22     --+-+-----+-+--------------+-+
                      23     +-+-+--------------+-----+---+
                      25       +-+-----+-+--+-+-+-----+---+
                      27         +--------------+-----+-+-+
                      28         +--------------+-------+-+
                      32         +-------+
                      34       +-+-------+--+-+-+-----+-+-+

Subadult female       14     --+-+-----+-+--+-+-+-----+-+-+
    (5)               15     +-+-+-----+--------+-------+-+
                      16     +-+-+
                      26         --------+------+-----+---+
                      33         +-----+------+-+-----+-+-+
```

\+ observed during the count
\- not observed but known to be still alive and marked during the count
[1] only a July and August count during 1989

Table 10
Roan population estimates for the Waterberg Plateau Park 1975-1990. See text for explanation.

population expansion phase

year	75	int*	76	77	78	79	80	int*	81	82	83	84
official	70	7	77	65	--	56	76	16	92	166	230	350
adjusted	70		77	80	85	88	100		141	176	220	275

int* = individuals introduced

annual growth rates (%) based on population estimates

year	75	int*	76	77	78	79	80	int*	81	82	83	84
official		10	-16			36		21	80	39	52	
adjusted		10	4	6	4	14		41	25	25	25	

int* = individuals introduced

population reduction phase

year	84	caught*	85	86	caught	87	caught	88	89	90
official	350	69	248	300	35	250	81	156	150	168
adjusted	275		210	245		215		156	150	160

caught* = individual removed and capture mortalities

Table 11
Best estimate of population composition and adult sex ratios

	M.ad.	F.ad.	M.sub	F.sub	juv	Tot.	sex ratio
1984	41	122	25	33	56	275	1 : 3.0
1985	46	77	16	32	40	210	1 : 1.7
1986	44	103	21	42	36	245	1 : 2.3
1987	43	95	14	17	46	215	1 : 2.2
1988	42	50	6	14	44	156	1 : 1.2
1989	40	47	19	24	22	150	1 : 1.2
1990	46	57	24	15	18	160	1 : 1.2

Table 12

Recruitment rates

	Adult females left	Adult females caught	Juv.	Pop. Tot.	Juv.:100 Fem.	Juv.as % pop.
1984	122		56	275	45.9	20.4
1985	77	25	40	210	39.2	19.0
1986	103		36	245	35.0	14.7
1987	95	21	46	215	39.7	21.4
1988	50	39	44	156	49.4	28.2
1989	47		22	150	46.8	14.7
1990	57		18	160	31.6	11.2
			average		41.1	18.5

Table 13

Summary of roan mortalities 1981 - November 1991

Cause	Juveniles			Subadults			Adults			
	Male	Fem.	?	Male	Fem.	?	Male	Fem.	?	
Unknown	1	1		2			5		1	10
Predation		1	2	1						4
Died on neigbours farm				1			1			2
Old age[1]							5			
Capture mortality				1			1	4		6
Total	1	2	2	5			12	4	1	27

[1] molar I worn right down

Table 14

Average mortality estimates October 1988 - August 1991 based on marked individuals (see p.22 for explanation)

Sex/age class	individuals	roan years	survivors	estimate
ad.females	17	57.0	15	3.5%
subad.females	4	2.7	3	37.5%
ad.males	11	49.3	3	18.03
subad.males	6	11.0	5	9.1%

3.4. Discussion

3.4.1. Population estimates - The **aerial census** figures from 1984 to 1988, fluctuate considerably and do not show a trend. The visibility fluctuations between the different months when censuses were undertaken, mask the actual population fluctuations (Figure 10).

A number of problems were experienced with the waterhole counts. Some observers made too few notes on individual unmarked animals to recognize all that drank more than once as duplicates. In the past this was often not done and individuals coming to drink repeatedly during a particular count were not recognized as doing so. This resulted in inflated population estimates. In the years preceeding this study, individuals recorded drinking repeatedly during a count were thought to constitute about 10%, compared to 60-80% in counts during the study. This was as a result of recognizing to few animals drinking repeately, with no artificially marked individuals. Animals were not always accurately aged and sexed, sexing of juveniles being particular unreliable. Also roan coming to the water at night were difficult to age and sex. Eartags could sometimes have been missed.

The waterhole count figures are considerably more constant than the aerial counts, when taking the captures into consideration (Figure 11).

Since roan drink regularly during the dry season and mainly during the day time, they can be fairly accurately counted, provided that care is taken to identify the individual animals.

Sex and age ratios

As sex and age ratios are based on the August waterhole counts, when the sample counted comprised most of the population, they should reflect those of the total population closely.

The age class composition compares well with that recorded by Joubert (1976) in the Kruger National Park (KNP) (Table 15). This author also used three age classes, but only included yearlings in the subadult age class. The comparison in Table 15 is based on seven years data from the Waterberg and four years from the KNP, where the roan population numbers ± 260 animals (Joubert 1976). In the KNP the recorded adult sex ratio was 1:1.9, while the sex ratio for adult sable antelope in the Matopos N.P., Zimbabwe, was 1:2.2-2.4 (Grobler, 1974).

The adult sex ratio in this study, was 1:3.0 before the captures but decreased to almost unity after 41 adult males to 85 adult females had been removed between 1985-1988. This narrowing of the ratio, is partly the result of capturing in a 1:2 ratio and, equally important, a higher survival rate among the adult males remaining after the capture operations. As sex ratios are determined by differential mortality (or loss to the population) of the two sexes, a relatively higher male mortality must be invoked to explain the wide ratio observed prior to the capture operations. Using the population model, the sex ratio would have changed from 2.9 to 2.0 females per male as a result of the captures only, assuming a female mortality rate of 0.095 and that for males of 0.1. For the ratio to narrow further, male survival must have increased. A possible explanation could be a reduced rate of intra-specific fighting, a potential mortality factor, as a result of the lower density of males after the captures.

The males were spread unevenly between the four clans (see Chapter 6). For three of the clans the average August adult sex ratio for 1988-1991 varied between 1.3 to 1.6 females per male. In the Duitsepos clan area the ratio was however, one male per 0.6 female or 182 males per 100 females.

3.4.2. Recruitment rates

Calving season: In this study a definite calving peak was recorded in the wet season, a fixed optimal birth season. This is in contrast to an unpredictable optimal season in very arid zones, depending on rainfall, or calving throughout the year in areas with little environmental change (Dott 1987, Skinner & van Jaarsveld 1987). On the Waterberg the calving season is in all likelihood determined by the pronounced cyclic fluctuations in nutrient levels of the sour veld (see Chapter 5). The calving peak observed in this study is in accordance with observations made on roan caught in the Kaudom Game Reserve, northeastern Namibia, were calving took place from the end of October to January (Hofmeyr 1974). In the Lambe Valley, Kenya, calving took place in November/December (Allsopp 1979), while Poché (1974) found that roan in Park W in Niger, calved in the early dry season, October to December. This is in contrast to the situation in the Kruger National Park and Percy Fyfe Nature Reserve, where breeding takes place throughout the year (Wilson 1975; Joubert 1976).

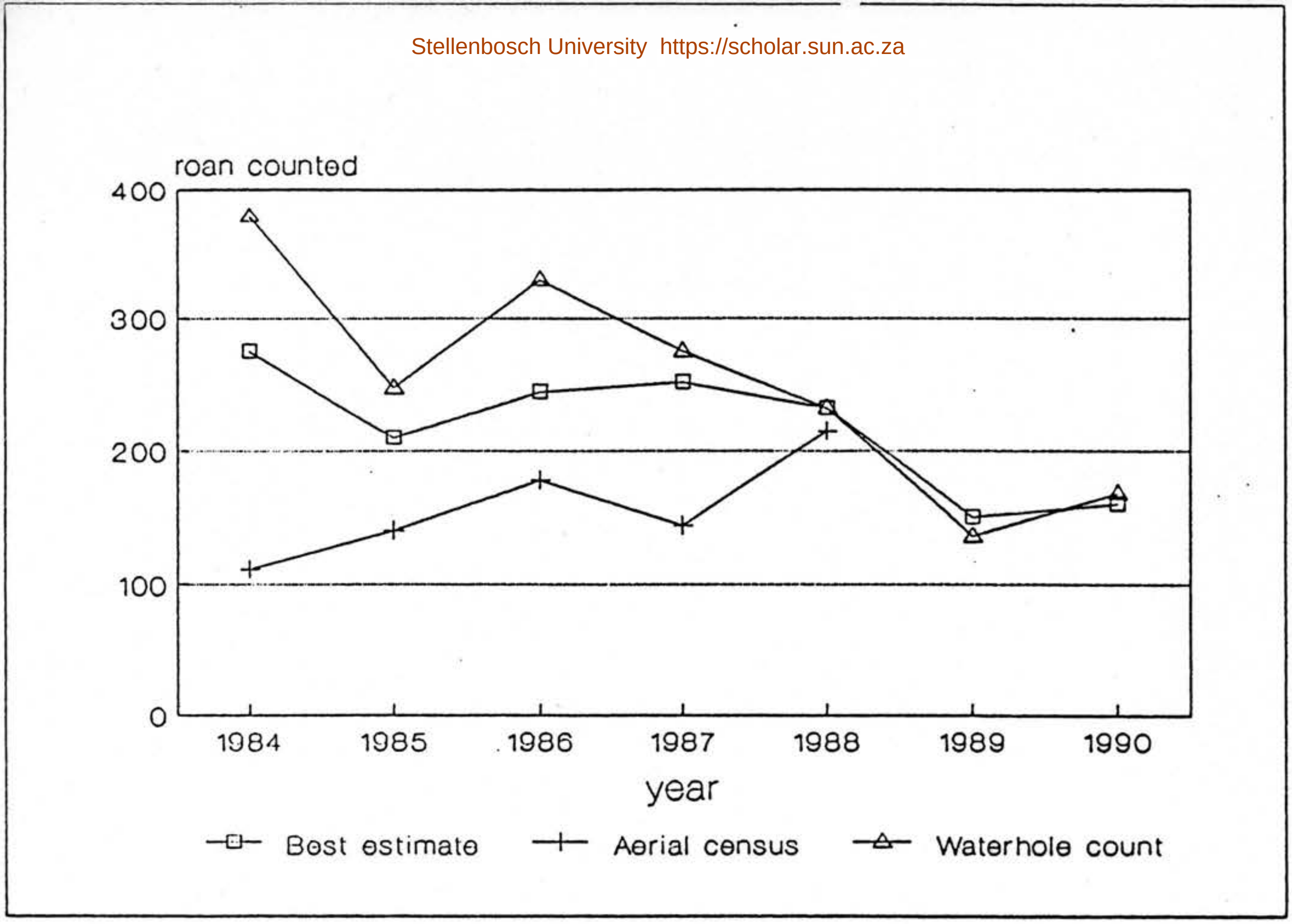
Table 15

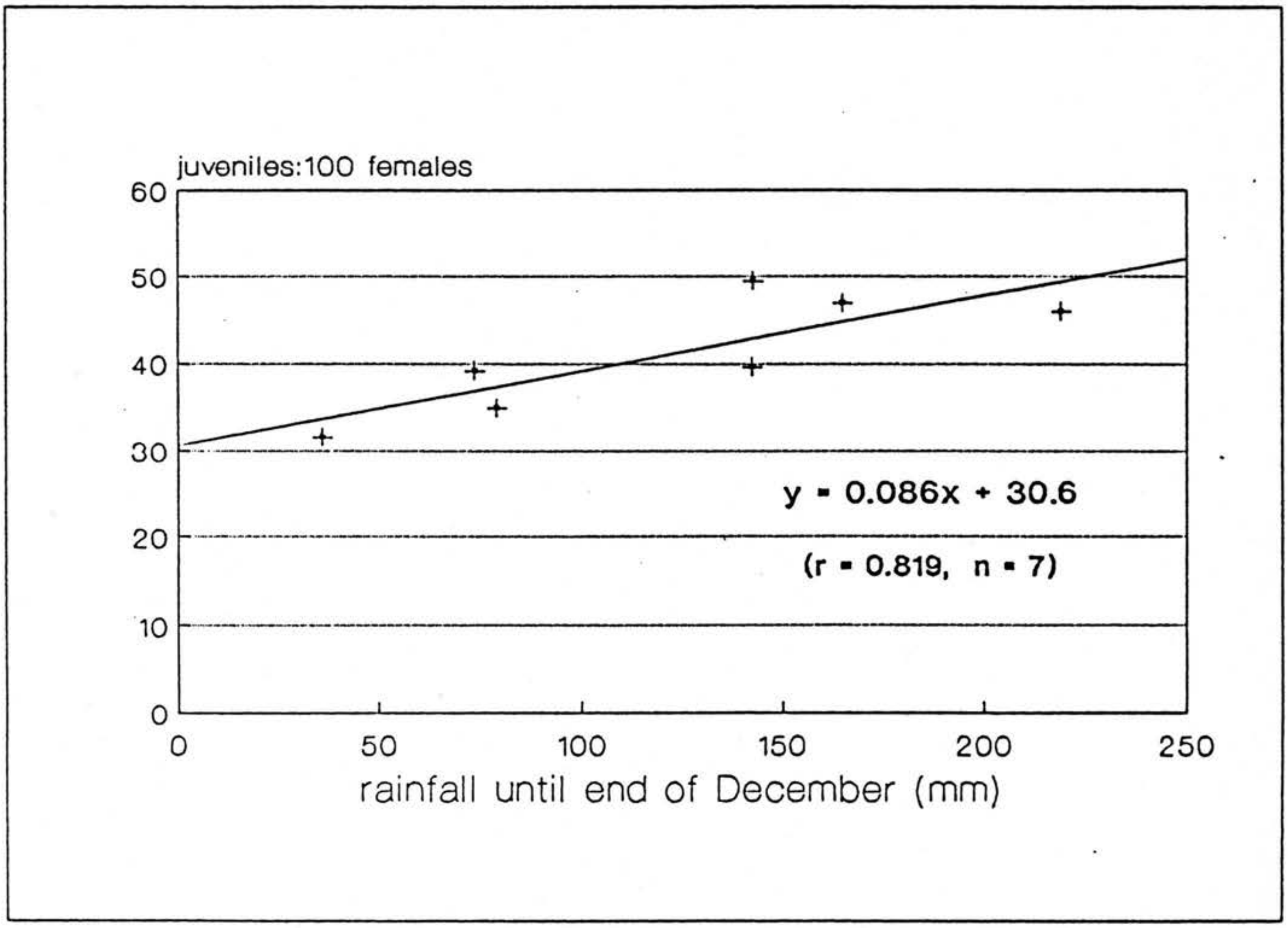
Comparison of population parameters between roan antelope from the Kruger National Park (Joubert 1976) and the Waterberg Plateau Park (this study)

		K.N.P.		Waterberg
Sex ratios				
Juveniles		1:1		1:1
Yearlings		1:1.2		1:1.5
Adults		1:1.9		1:1.8
1984 before captures				1:3.0
1989 after captures				1:1.2
Age structure				
Juveniles	average	19.7%	average	18.5%
Adults	"	62.8%	"	60.4%
Adult females	"	41.7%	"	38.0%
Calves:100 ad.females	"	39.2	"	41.1
	range	(18.1-72.5)		(31.6-49.4)

Figure 11: A comparison between the waterhole counts, the aerial census and the best estimate.

Figure 12: The relationship between early season rainfall and juvenile-female ratio in August.


roan counted
400
300
200
100
0
1984
1985
1986
1987
1988
1989
1990
year
Best estimate
Aerial census
Waterhole count


juveniles:100 females
60
50
40
30
20
10
0
0
50
100
150
200
250
rainfall until end of December (mm)
y = 0.086x + 30.6
(r = 0.819, n = 7)

Wilson (1975) observed that sable antelope in Transvaal nature reserves calved from January to March, with a peak in February. For young females calving for the first time it could be as late as June. This agrees with sable antelope on the Waterberg, where the majority of calves are also born between January and March. It would appear that this is a more favorable period to calve, since the female has the benefit of the first green flush during the last third of the gestation period and green grass is available in abundance, once the calf is born. Weaning takes place after six months in the dry season.

Calving success: The apparent calving success/early survival was slightly better in the Waterberg than in the KNP, 41.4 calves per 100 adult females as against 39.2. However the range recorded on the Waterberg was much narrower than in the KNP (Table 15). Grobler (1974) recorded 56-67 calves per 100 adult sable cows in the Matopos N.P.

Between 1988 to 1991 the Geelhout/Huilboom clan produced more calves than expected compared to the whole population. The difference was not significant (chisquare = 3.238, 3 d.f., P=0.36).

The relationship between early season rainfall and calving success can be explained as follows: Roan start to calve as early as August, when the veld is still dry. If it rains well in September/October, the sprouting green grass provides lactating cows with the necessary protein. Demand for dietary protein quadruples during late pregnancy and early lactation (Moen 1973, Sinclair 1974b). This green flush is especially important, since the plateau is essentially sourveld, characterized by a significant drop in grass quality during the dry season (Chapter 5).

Positive relationships between early season rainfall and the subsequent calf crop have also been reported for wildebeest in the KNP (Mason 1990) and buffalo in the southern Serengeti (Sinclair 1974b).

3.4.3. Mortality

The mortality rates recorded during the study are relatively low while the differential between age and sex classes corresponds to that found in other ungulate studies. For example, kudu which, like roan, reach an age of about 14 years in the wild, exhibited the following average yearly survival rates in the KNP: juveniles 0.45, yearlings 0.84, prime subadult/adult females 0.91 and old adult females 0.80. Male survival between 2 and 5 years of age averaged

0.8 and at 6 years and older dropped to 0.50 (Owen-Smith 1984, 1990).

Joubert (1976) found that small calves in the KNP experienced a high initial mortality, caused *inter alia* by cytauxzoonosis, which occurs enzootically in the reserve, and babesiosis. These blood parasites have as yet not been diagnosed as a mortality factor on the Waterberg. Here mortality seems mainly due to the loss of calves born early in the season. They are probably underweight from the start and if the rains start late they are undernourished and susceptible to disease. No direct evidence could be found for this statement but several indirect observations support it. Firstly, cows are in bad condition during this time of the year and unlikely to be able to mobilize sufficient body reserves to feed a small calf adequately during the initial two or three months. White (1978) recognizes nutritional adequancy of the very young through maternal nutrition as a major factor influencing the survival of the offspring. Secondly the relationship between early rainfall and, through this, improved nutrition and the subsequent calf crop, also points to this cause of mortality. Male calves generally have higher metabolic needs than females, they suckle more often and also grow faster. This has been observed in red deer and elephant (Moss 1988). My data set was too small to show whether there was a higher mortality rate among male calves in years with a long dry season, as has been observed with elephant.

Joubert (op.cit) observed an increased mortality among young males, coinciding with their eviction from the breeding groups. The same was observed in the present study, but no definite causes could be identified. From 1981-1990, five subadult male deaths were recorded, but none for subadult females. A higher predation risk and injuries from fighting probably play a role. Although no mortalities due to intra-specific fighting were recorded, several injuries, probably as result of fighting, were seen amongst males. Three adult males were observed to be blind in one eye and another was blind in both eyes. No blindness was observed in females. An adult male which was destroyed because of his poor condition, had several broken ribs, which had started to heal.

Adult males experienced a higher mortality rate than females. In a small sample (n=11) predation was responsible for the death of 2.6 males per female.

Known mortality due to predation in the KNP amounted to 1.6% of the roan population (Joubert 1976). Such a low predation level, even when affecting more males than females, can not be responsible for the skewed sex ratio recorded in the KNP. That males are more at risk from predation has been shown in several studies, for example in kudu (Hirst 1969), and buffalo (Sinclair 1974a). However several studies indicate that this disparate sex ratio, in favour of females, is not the result of sex selective predation alone. For kudu in the Andries Vosloo Kudu Reserve, Allen-Rowlandson (1980) recorded a sex ratio of 1:2.2 for animals at least one year old in the absence of large predators. In this study, subadult and adult males also expericened a higher mortality rate in the absence of predation.

Chapter 4: The population model

4.1. Introduction In order to judge to what extent the study population was under environmental stress, I had to compare it to a benchmark population - one in an optimum habitat. However detailed data on roan antelope population dynamics was not available for such a comparison. Previous studies have been undertaken in marginal habitats and none has been devoted to a population of a comparable size in optimum habitat. To overcome this problem, I resorted to population modelling.

The aim of the computer model was to simulate the dynamics of the study population in order to understand the effects of possible limiting factors and of captures and introductions, but also to project future population responses to management actions, discussed in Chapter 7.

Exploratory modelling was used to determine the effect of the different population parameters. The models are deterministic, that is, all parameters used are known, in contrast to a stochastic model where parameters are selected at random from a certain range.

Models to simulate populations dynamics have been used *inter alia* by Starfield & Bleloch (1986) for roan, Starfield *et al*. (1979) for impala, Berry (1981) and Starfield *et al*. (1976) for wildebeest and for lion by Venter and Hopkins (1988).

4.2. Method Two related population dynamics models were developed for use on a personal computer. They are both spreadsheet based and simulate on an annual basis, ie. with a time step of one year, the late dry season (August) roan population. See Appendix 3 for an explanation of how to use the models.

Both models make use of eight age/sex classes, namely young of the year, yearlings, two-year-olds and adults for each sex. These sex/age classes are used as the modelling units. Mortality rates are applied as a yearly average for a particular age/sex group. The number of roan introduced or captured could be changed for each individual year and age/sex group.

The models differ in certain aspects. Model 1 attempts to simulate the population between 1975-1990. An average fecundity rate is applied, since it is virtually impossible to obtain an actual annual fecundity rate from field data.

Model 2 is a refinement of the first model and makes use of the more detailed age/sex data available for the period 1984-1990. Model 2 makes use of the same assumptions, but in addition the influence of rainfall during the first half of the season, which has an effect on the calf to adult female ratio (Chapter 3), is incorporated.Instead of estimating a fecundity rate and early calf mortality separately, which is difficult and unreliable, the number of calves per 100 adult females in the population during the August waterhole count is used in this model. The calf to adult female ratio can be adjusted by a constant, starting from a particular year, to explore the possible positive influence of, for example, feeding lick, on population growth. Both models are presented schematically in Figure 13.

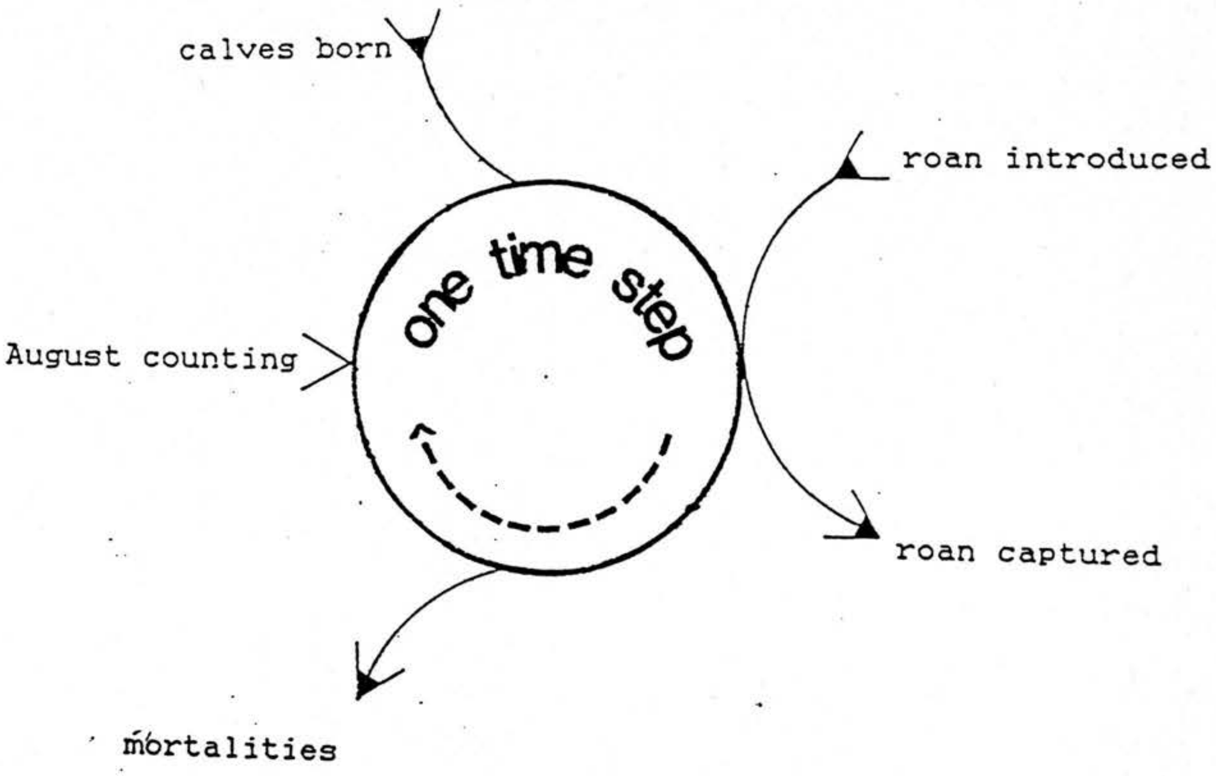
The following assumptions have been made:

1. Average values apply to the entire population, no allowance is made for intergroup differences.
2. The population will not be allowed to reach ecological carrying capacity (ECC), due to the capture program. ECC is in excess of 300 roan.
3. Rainfall does not seem to exert a definite clear influence on the population, so that its inclusion as a parameter in the model (Model 1 only) is not justified.
4. Predation pressure is minimal, as long as alternative prey is abundant, ie. warthog, kudu, steenbok and duiker.
5. The majority of cows have their first calf when 32-34 months old. Cows in their third year will not yet have a calf in attendance when counted in August.
6. The social behaviour of the roan is not considered in the models.
7. Captures and introductions take place before August during any particular year.

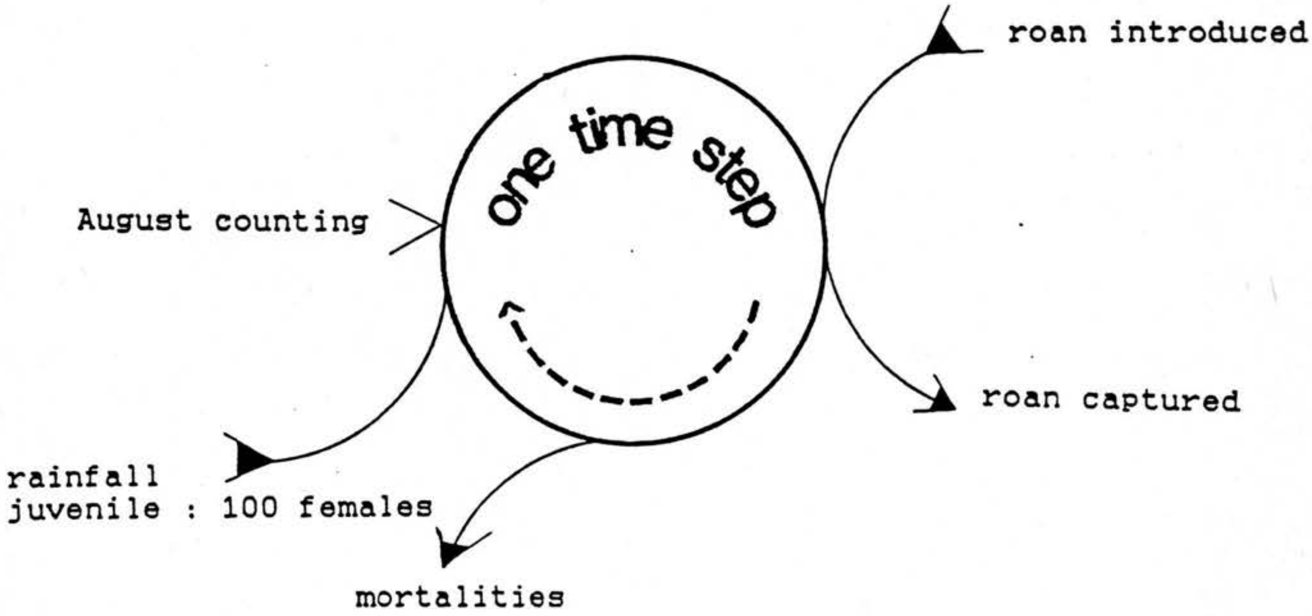
Maximum/minimum values have been selected for some of the parameters. For example, a minimum average mortality rate is taken to a function of longevity, based on population dynamics data in Chapter 3.

Figure 13: A schematic representation of population dynamics models 1 and 2.

Model I



Model II



The models were "tuned in" (Starfield et al. 1976) by applying realistic values to model parameters and changing them to obtain a reasonable fit with the actual census data, making use of regression analysis. "Realistic values" to start with are based on the data in chapter 3 and the population manipulations that took place.
For the sensitivity analysis the input parameters of Model II were changed by 5, 10 and 15% of the original value. All other parameters were kept constant, the simulation was run and the change to the population by the year 2000 was noted for each altered parameter. For the sensitivity analysis, mortality was reduced and fecundity increased to achieve a faster simulated growth rate, in order to simplify comparison of the effects of these changes on the different parameters.

4.3. Results

4.3.1. Population size estimates The standard input parameters used for both models are shown in Tables 5 and 6 and Appendix 3. All simulations are based on these input variables, except where otherwise stated. Both models predict total population size for the different years reasonably well. The correlation coefficients for the regression analysis between the simulated and observed (Chapter 3) population parameters are presented in Table 16. The modelled population size is compared to the best estimate in Figures 14 and 15 for models I and II respectively.

4.3.2. Age and sex ratios The two models fit the observed subadult/ adult female data more closely than that for the males (Table 16). When adult and subadult females are lumped, the correlation coefficients are higher, than when the two age classes are modelled separately. The improvement of Model II over I is only slight for the subadult/adult females. The simulation output for subadult/adult males is considerably better using Model II, when both age groups are lumped. The correlation coefficients for adult males alone are very low with both models.
Model II simulates the juvenile age group somewhat better than the simpler Model I, by taking the rainfall/ juvenile relationship into consideration.

4.3.3. Recruitment rates Average fecundity rate for adult females for Model 1 was taken as 97%, with initial juvenile

mortality as 25%. For model II the early season rainfall and the calves per 100 female ratio (Chapter 3) were used. The actual ratio of calves per 100 females from 1984 to 1990 varied between 33.7 to 46.7, average 40.7.
In each case the number of females prior to a capture, but with mortality subtracted, was used for the calf to female ratios.

4.3.4. Mortality rates The mortality rates used in the two models are given in Appendix 3. No juvenile mortality rate was applied in model 2. Instead I made use of the juvenile to adult female ratio observed in August. The average mortality rates applied per age/sex class are a simplification of the real system, where mortality rates fluctuate between years.

4.3.5. Sensitivity analysis The results of the analysis are given in Table 17. It is clear that female mortality rate and the juvenile to adult female ratio are important parameters, since they have the greatest effect on population growth rate or the output data as tested. In contrast, male and subadult female mortality rates were fairly insignificant in determining model output data.

Table 16

Correlation coefficients (r) for the regression analysis between the simulated and observed population parameters

Regression models	Model 1	Model 2
	r values	
Population size 1975-1990	0.948	
Population size 1984-1990	0.984	0.984
Adult and subadult males	0.133	0.618
Adult males	0.241	0.182
Subadult males	0.130	0.674
Adult and subadult females	0.964	0.970
Adult females	0.872	0.907
Subadult females	0.089	0.096
Juveniles	0.736	0.958
Juveniles:100 adult females	0.205	0.859

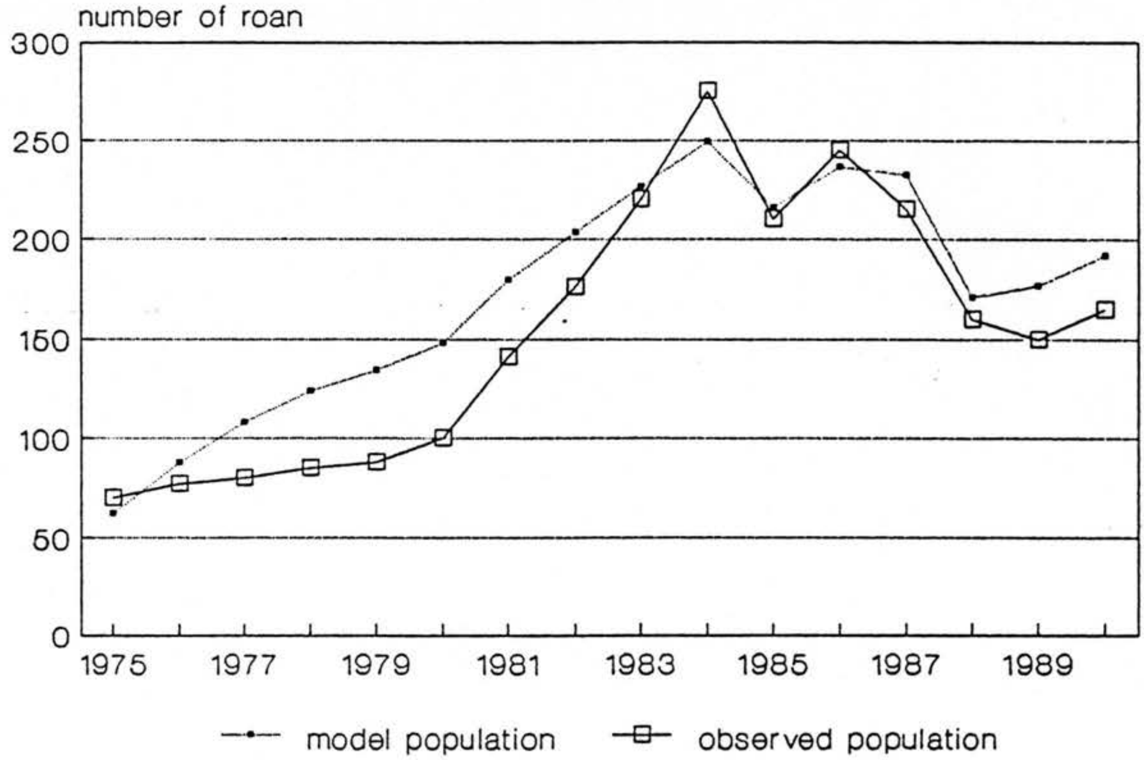
Table 17

Model II input parameter sensitivity analysis through percentage change of the original parameter value and expressed as change in population size in the year 2000.

parameter	% change	Pop. change
Subadult male mortality	- 5%	3
	- 10%	7
	- 15%	10
Adult male mortality	- 5%	2
	- 10%	4
	- 15%	7
Subadult female mortality	- 5%	5
	- 10%	9
	- 15%	14
Adult female mortality	- 5%	18
	- 10%	37
	- 15%	56
Juvenile to adult female ratio	+ 5%	30
	+ 10%	61
	+ 15%	96

Figure 14: A comparison between the model 1 output and the actual population estimate, 1975-1990.

Figure 15: A comparison between the model 2 output and the actual population estimate, 1984-1990.


number of roan
300
250
200
150
100
50
0
1975
1977
1979
1981
1983
1985
1987
1989
model population
observed population

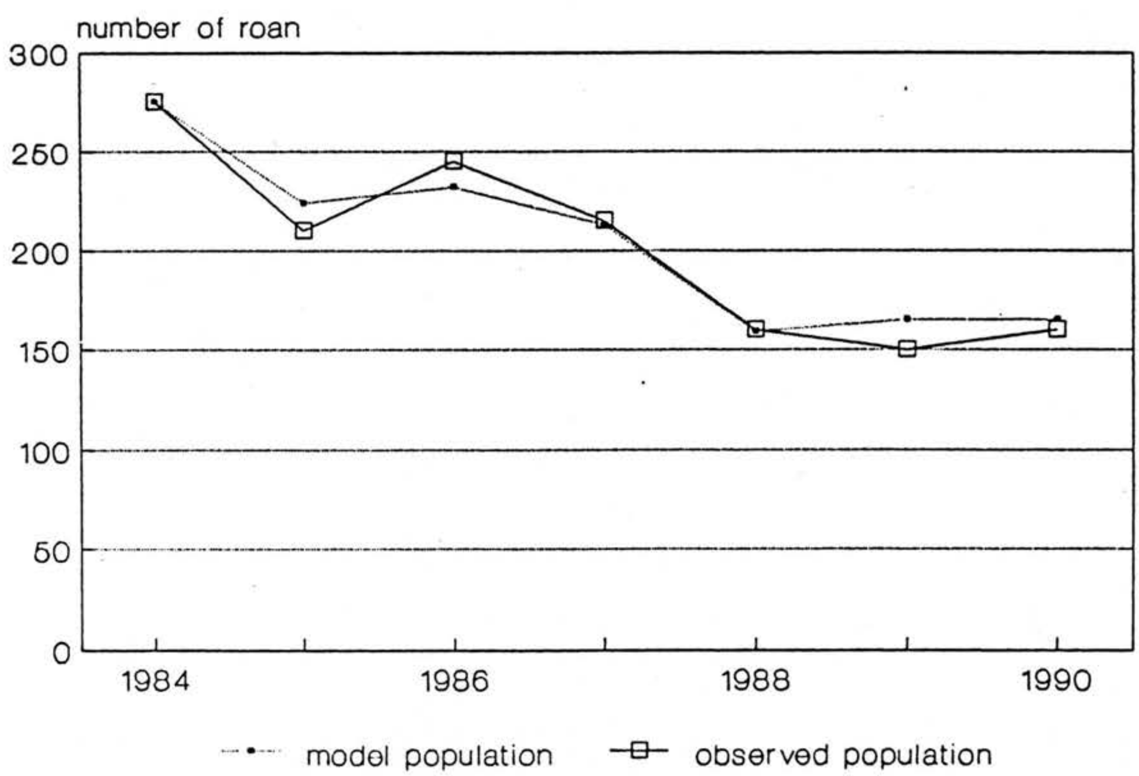
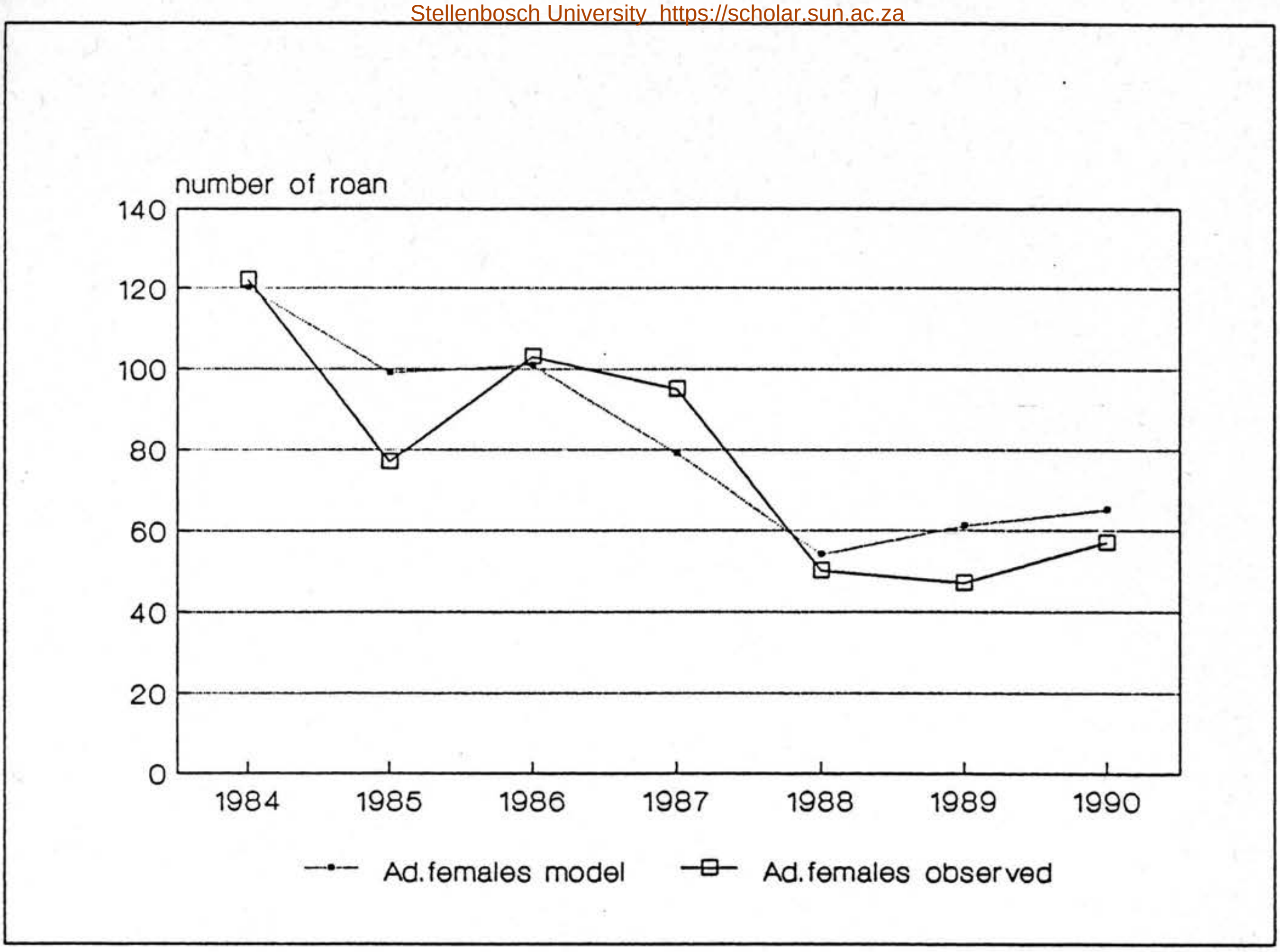

number of roan
300
250
200
150
100
50
0
1984
1986
1988
1990
model population
observed population

Figure 16: A comparison between the model 2 output and the actual adult female estimates, 1984-1990.

Figure 17: A comparison between the model 2 output and the actual adult sex ratio estimates, 1984-1990.


number of roan
140
120
100
80
60
40
20
0
1984
1985
1986
1987
1988
1989
1990
Ad.females model
Ad.females observed

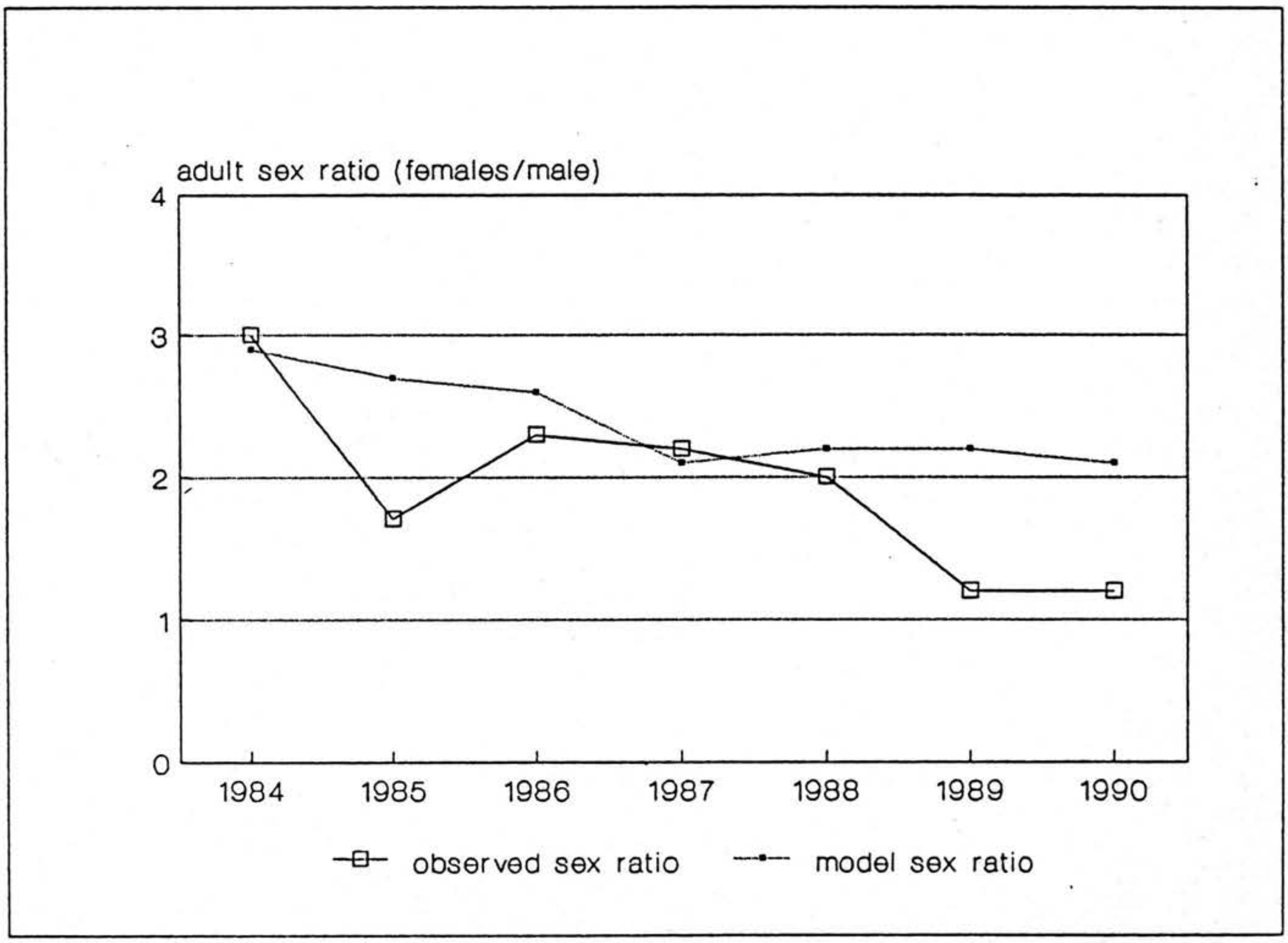

adult sex ratio (females/male)
4
3
2
1
0
1984
1985
1986
1987
1988
1989
1990
observed sex ratio
model sex ratio

Figure 18: A comparison between the model 2 output and the actual roan juvenile estimates, 1984-1990.

Figure 19: A comparison between the model 2 output and the actual juvenile per 100 adult female ratio estimates, 1984-1990.

4.4. Discussion The population dynamics of the roan antelope on the Waterberg were successfully modelled, judging by the good correlation coefficients obtained for the period 1984-1990.

In all cases, except for adult males, Model II equals or betters the simulated values of Model I, when compared to actual field data. This was expected, since Model II incorporates the limiting factor, early season rainfall, which fluctuates annually and was applied in the model.

There is a good correlation between the model output and observed numbers of adult and subadults grouped, for either sex. However if the two age groups are separated, the good correlation is lost for adult males and subadult females (Table 16). The most likely reason, is believed to be inaccurate ageing of individual animals during the counts. This assumption is supported by the observation that marked animals were incorrectly aged by field staff. The male simulations were the least accurate (Table 16). This discrepency may be partly due to inaccurate counting since solitary males are generally more difficult to recognize as individuals, compared to females in breeding groups. Dominant males come to water repeatedly during a count, for example one male came to the waterhole 12 times during a 72 hour count, four of the visits being at night. During four full moon counts in August (72 hours), 76% of adult males and 96% of the adult females known to be in the population were recognized on average. Thus the effectiveness with which individual males were recognized, probably varied more between different counters and between counts, than in the case of females.

Although the population is simulated well by the models for the study period, when realistic input parameters are used, it is expected that certain factors that can influence population dynamics significantly, have not been incorporated. The study period was relatively short and the data set is not detailed enough to present a complete picture. However a start has been made with the present model. The roan population now needs to be monitored on an ongoing basis and the data collected must be compared to the simulated parameters. Other environmental factors that have an effect on the population, need to be identified and incorporated in the model.

Chapter 5: Nutritional aspects

5.1. Introduction

For most animals nutrition is probably the single most important factor that determines their abundance. For herbivores quantity itself seems less important than quality and especially the crude protein content (Sinclair 1974b, Stanley Price 1978, White 1978, Owen-Smith & Novellie 1982). The successful management of wild ungulate populations requires an understanding of their feeding requirements, both at the plant species and individual key nutrient level. Feeding requirements change seasonally and are dependent on factors such as age and the reproductive stage of the individual.

The Kalahari sands, occuring in the northeast of Namibia as well as on the Waterberg plateau, are considered to be "highly leached dystrophic acidic sands" (Huntley (1982). It was thus suspected, that certain nutrients might be deficient. The aims of my study were thus, to establish general trends of grass species selection and to draw up macro-nutrient budgets for protein, calcium and phosphorus. Trace minerals deficiencies were also investigated.

Detailed feeding studies, focussing on grass species selection, have been undertaken for both roan and the closely related sable antelope (Wilson 1975, Joubert 1976, Grobler 1981). These indicate that roan select climax grass species with a high nutrient content, grasses that are green and those that have a high leaf to stem ratio. Since roan are predominantly grazers (see Chapter 2) I focussed on grass species selection and collected browse observations opportunistically.

Diet quality for ruminants can be determined from fistulated animals, rumen samples, direct vegetation analysis or faecal

analysis (Erasmus _et al_. 1978, Putman & Hemmings 1986, Holecheck _et al_. 1982).
Fistulas are expensive and impractical to use on free ranging ungulates. To obtain rumen samples one needs culled animals and the effects of digestion on sample composition is difficult to determine. Analyzing hand selected plant material is unreliable because of differences in selectivity between animal and investigator ('tMannetje 1984, Fourie _et al_. 1986, O'Reagain & Mentis 1988). Nonetheless mineral levels in the soil (because of their influence on the vegetation) and in hand selected vegetation were determined for comparison with samples collected elsewhere.
Faecal chemical analysis is a very useful alternative method of determining diet quality. Erasmus _et al_. (1978), Putman and Hemmings (1986), Leslie & Starkey (1985), Stanley Price (1977), Renecker & Hudson (1985), Mould & Robbins (1981) and Belonje and van den Berg (1980a&b) _inter alia_ showed that a linear relationship exists between the dietary and faecal chemical composition for certain nutrients, including N (crude protein), P and Ca.

5.2. Methods

The soil analysis data in Jankowitz (1983) was mapped and statistically analysed.
Grass species selection was determined by observing where roan had been feeding and then back-tracking on the spoor. The species utilized were noted as well as the number of tufts of all species found within a one meter radius around the utilized tuft. Tufts within this circle were considered to be available to the roan. Grass and bite heights were also noted. An effort was made to sample 25 utilized tufts per feeding track. This method could only be used on green grass, where fresh bites could be distinguished from old ones. A selection index based on the fraction of utilized tufts per species was calculated from this data.
Grass samples for chemical analysis were collected from 14 sampling localities spread over the plateau (Figure 20). Sites were selected to cover different habitat types, both preferred and avoided by roan. In the 1989 wet season _Digitaria seriata_, a grass selected by roan, was the only species sampled. To obtain an abundance index, the clipped grass collected in a five minute period was weighed.

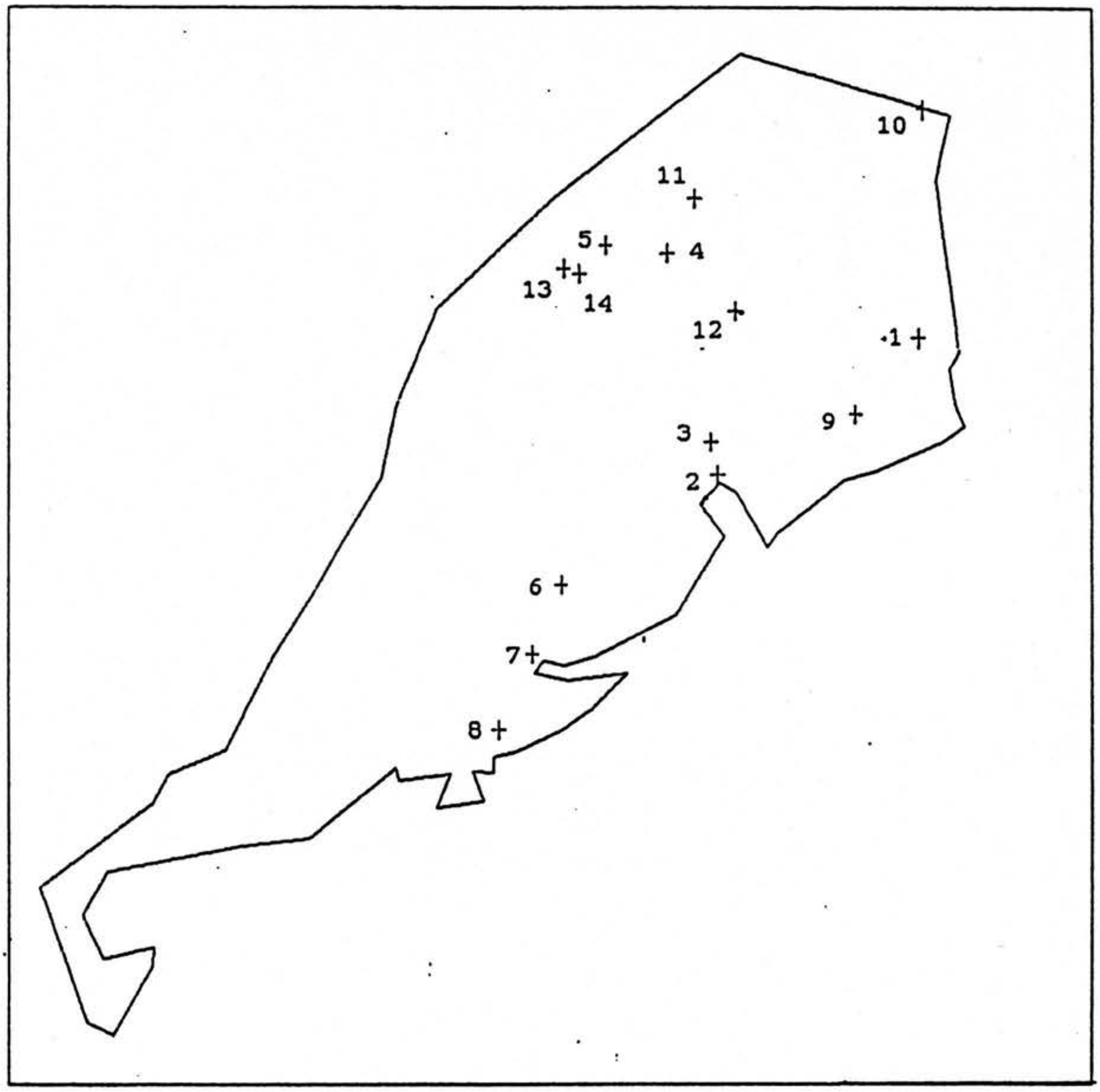


Figure 20: Grass sampling localities on the plateau.

The objective was to simulate a grazing roan antelope while collecting the sample. Grass was sampled in this way and not by clipping random quadrants, to obtain an index of the potential ingestion rate of a roan feeding on these clumped tufts.
In the dry season Panicum kalaharense and Brachiaria nigropedata were also sampled in the same way. A subsample of the grass was air-dried and chemically analysed in the Windhoek Agricultural Laboratory.
I sampled the two main vegetation types in that part of the plateau important to the roan in the dry season. In September 1988 25 one m^2 quadrants per habitat were clipped at a representative site. Quadrants were laid out in a U-shaped transect and 25 meters apart. The fresh weight of each species was determined per quadrant. Moisture content was between 10 and 30%.
Faecal samples were collected opportunistically when a roan was observed defaecating in the field. The animal's age/sex class and locality were noted for each sample collected. Rectal faecal samples were collected from 20 roan ear-tagged/ collared in October 1987, 3 females eartagged in March 1988 and 7 roan captured in July 1988.
Four roan were kept in the boma after the 1988 capture operation, as possible replacements for capture mortalities. These animals, a adult male and female, a yearling female and calf born in the boma, consumed a bale (appr. 25 kg) of good quality lucerne per day. They had free access to water. Faecal samples from the adults were collected after the animals had been feeding on lucerne for four weeks.
Blood/serum samples were collected from 20 roan in October 1987 and from 31 in July 1988. Two liver samples were available for trace mineral analysis.
Faecal samples were air-dried, blood/serum and liver samples were frozen after collection and analysed at the Windhoek Agricultural Laboratory. The methodology is described by Grant (1989).
Visual condition estimates on a five point scale, were made primarily during the waterhole counts, using the criteria described by Berry and Louw (1982) for wildebeest.
Observations on drinking behaviour are primarily based on waterhole counts during the dry season, lasting for 48 or 72 hours.
The Statgraphic statistical package was used to test for differences between nutrient concentrations, by making use of the one way analysis of variance multiple range test with 90% and 95% confidence intervals.

5.3. Results

5.3.1 Feeding behaviour

Species selection - Grazing The observations in Table 18 are based on feeding records from 8 different animals, collected between April and June, in other words in the late wet and early dry seasons. The data is thus by no means representative for the whole year., It merely serves to illustrate that roan antelope select for climax grasses. The grass species utilized, apart from the *Eragrostis jeffreysii* and *Aristida stipitata*, are considered climax grasses for this area. Of those not utilized, only *Eragrostis pallens* is a climax species, but it is a very hard grass. In the wet season roan fed at times exclusively on *Digitaria seriata*, but this grass dries out very quickly and is then rejected in favour of species such as the *Panicum* which remain green. Feeding height in relation to grass tuft height was measured for some of the selected grass species and the measurements are given in Table 19. Feeding height corresponds to the height on the tuft, down to which the antelope can bite off leaves only. On tufts with a lot of fine leaves at the base and only few culms in the center, for example *Triraphis schinzii*, the roan fed down to a much lower level than for example on *Digitaria*, which becomes very stemmy towards the base.

Browsing Roan antelope were observed to browse on the following trees or bushes: *Grewia reticulata*, *Lonchocarpus nelsii*, *Acacia ataxacantha* and *Ochna pulchra*. Browsing was recorded between April and November, when the grass was dry and browse was still or again green. Only the new foliage of *Ochna pulchra* was eaten. Leaves of *Grewia* were stripped from the branches; a roan would take about 30cm of branch into its mouth and pull the leaves off along it. Most browsing took place at neck height.

5.3.2 The availability of key nutrients to roan

5.3.2.1. Soil nutrient concentrations - The values for the plateau are averages derived from 55 soil samples analysed by Jankowitz (1983). These nutrient concentrations for the different vegetation types were subjected to a multiple range analysis, producing two homogeneous groups, one relatively nutrient rich and one poor. The nutrient rich (rocky) group is from the rocky perimeter and the Slangkloof/Sjamarawa valley drainage line. The central sandy plateau forms the relatively nutrient poor (sandy) group.

Table 18

Grass species selection index
(see text for explanation)

	tufts utilized	tufts available	% of tufts grazed
Brachiaria nigropedata	36	108	33
Panicum kalaharense	27	103	26
Eragrostis jeffreysii	27	113	24
Andropogon schirensis	15	35	43
Triraphis schinzii	11	33	33
Digitaria seriata	11	180	6
Schizachyrium sanguineum	1	2	50
Aristida stipitata	1	137	1
Eragrostis pallens		60	
E.rigidior		58	
Stipagrostis hirtigluma		50	
S.uniplumis		47	
Aristida meridionalis		22	
Tricholeana monachne		8	
Melinis repens		6	
Aristida congesta		5	
Pogonarthria squarrosa		3	
Aristida mollissima		1	
total	129	971	

Table 19
Feeding height in relation to grass tuft height (in cm)

	Feeding height			Tuft height		
	x	SE	n	x	SE	n
Digitaria seriata	26.5	8.4	10	63.5	16.7	10
Eragrostis jeffreysii	20.0	5.6	27	64.8	20.6	27
Brachiaria nigropedata	13.9	4.2	35	39.9	18.3	35
Panicum kalaharense	10.2	3.9	25	78.3	42.3	24
Andropogon schirensis	9.0	3.7	15	66.7	25.6	12
Trirapsis schinzii	8.1	2.4	8	43.3	24.9	6

Table 20
Nutrient concentrations and pH in the soil of the two homogenous groups, based on raw data from Jankowitz (1983) and Jankowitz & Venter (1987)

Homogenous group	n	pH	P	Ca	K	Mg
				average values (ppm)		
rocky	10	4.8	20.5	258.0	58.0	62.5
sandy	45	4.2	5.0	35.6	24.3	9.0

These values all differ significantly between the two groups (multiple range test, 95% confidence intervals).

Nutrient concentrations and pH, which all differ significantly (confidance intervals 95%) between the two groups, are given in Table 20.

5.3.2.2. Availibilty in the forage - **Grass biomass** Although my sample size is small, it is considered adequate in conjunction with the very similar data from Jankowitz, to show that grass quantity itself is not limiting (Table 21, Sec. 5.5.2.2.).
The abundance index for species Digitaria, Brachiaria and Panicum, obtained while sampling grass for the qualitative analysis at the 14 localities, is given in Table 22.

Protein - Protein content of Digitaria seriata was determined from the 14 sampling localities, during active growth in January, when mature in March and dry in August (Table 23). In March the average crude protein content was significantly different ($P<0.0001$) between the rocky areas (12 ± 1.6%), and the sandy habitats (7.2 ± 0.7%).
In August, three preferred grass species, Brachiaria nigropedata, Digitaria seriata and Panicum kalaharense, were compared with regard to their crude protein content. Panicum had a higher crude protein content than Digitaria ($P<0.1$), and that of Brachiaria was intermediate (Table 23).
Green grass shoots on a burned block had a crude protein content of 20% in September, when the shoots were 5 cm long.

Phosphorus and calcium concentrations were determined for Digitaria during the three growth stages and for all three species in August, as for crude protein. The data is presented in Table 23. Differences were not significant.
The average Ca : P ratio for the Digitaria samples was 2.2 ±0.2 : 1 in January, 7.5 ±3.1 : 1 and in August 10.2 ±6.4 : 1. The Ca/P ratios were similar in the other grasses analyzed.
Grasses were not analysed for trace minerals.

5.3.2.3. Nutrient status of the roan - **Faecal analysis** 6 dung samples from the adult animals kept in the boma were analysed. Faeces were collected from free ranging roan throughout the year, 7 samples (3 from the rectum) in February/ March (the wet season) and 10 (7 from the rectum) from July to September (the dry season). 20 rectal samples were taken during the October marking operation.

Table 21
Grass biomass in 1980 and 1988 in the four major vegetation types

Vegetation type	area (ha)	Grass Biomass (kg/ha) May	September	September 1988
		Jankowitz (1983)		this study
A	4 679	808.4	630.5	713.6
B	23 349	736.5	580.2	792.8
C	185	946.0	569.4	---
D	10 662	432.8	422.3	---

A=Terminalia sericea–Thesium megalocarpum tree/shrub savanna
B= " " –Melhania acuminata " " "
C=Anthephora pubescens–Eragrostis superba grass savanna
D=Peltophorum africanum rock communities

Table 22
Grass quantity (g/5 min fresh weight) for 14 sampling sites

		Digitaria		Brachiaria	Panicum
	January	March	August	August	August
avg±std	91 ± 12	158 ± 93	81 ± 12	86 ± 8	92 ± 6
range	66 – 100	25 – 350	50 – 93	70 – 93	81 –100

Table 23
Nutrient concentrations in grass samples
(% of dry mass)

		P	Ca	Prot
January	avg±std	0.15 ± 0.01	0.32 ± 0.04	17.81 ± 1.60
Digitaria	range	0.13 – 0.17	0.27 – 0.39	15.71 –20.97
	n	c[1] 6 C	a 8 A	d 12 C
March	avg±std	0.09 ± 0.03	0.59 ± 0.18	8.80 ± 2.51
Digitaria	range	0.04 – 0.14	0.44 – 1.13	5.98 –14.49
	n	b 12 B	b 12 B	c 12 B
August	avg±std	0.03 ± 0.01	0.24 ± 0.10	2.85 ± 0.49
Digitaria	range	0.01 – 0.06	0.13 – 0.46	2.10 – 3.89
	n	a 14 A	a 14 A	a 14 A
August	avg±std	0.02 ± 0.01	0.24 ± 0.11	3.48 ± 0.63
Brachiaria	range	0.01 – 0.04	0.12 – 0.48	2.80 – 4.60
	n	a 8 A	a 8 A	ab 8 A
August	avg±std	0.03 ± 0.01	0.22 ± 0.09	3.78 ± 1.13
Panicum	range	0.01 – 0.05	0.07 – 0.34	2.27 – 5.48
	n	a 11 A	a 11 A	b 11 A

[1] Letters show results of multiple-range tests. Different letters indicate a significant difference, small letters 90% confidence intervals and capital letters 95%.

Results of chemical analysis are given in Table 24. Faecal P content is significantly higher in wet than in dry season samples and is similar to values obtained from animals in the boma.
The calcium concentration is also higher in the wet season samples than in those from the dry season. The animals being fed lucerne had faecal Ca levels more than twice those of free living animals in the wet season. The crude protein content of faeces was higher in the wet than in the dry season, but both were lower than the October samples and similar to those from animals in the boma.
Blood and serum samples 20 samples collected in October were analysed for blood selenium and serum copper and zinc. Average values for the age/sex groups are given in Table 25. 31 serum samples were collected in July 1988 and analysed for copper, zinc, calcium and phoshate and the results are given in Table 26.
Adult males had a higher blood selenium level than adult females or subadults. In July adult females had the lowest serum copper concentration, 1.35 ppm as compared to 1.51 ppm for subadults. This difference was significant (multiple range test, 90% and 95% confidence intervals). The serum copper values of adult males were intermediate. However when October and July samples were grouped, no significant differences were found between the age/sex groups. Serum phosphate levels followed the same pattern as those for copper in July (see-Table 25).
No significant age or sex differences were found for calcium and zinc.
Liver analysis Samples from two old males, that were shot, were analsed for trace minerals, the results being as follows: copper 348-502 mg/kg, iron 324-372 mg/kg, zinc 194-236 mg/kg and manganese 10-12 mg/kg.

Visual condition index In June, 12 adult males had an average condition index of 3.4. In August the mean for 32 males was 3.2. While all males had an index of 3 or 4 in June, that for four males in August was only only 2.5 although the value for the majority was 3. Adult females had a average condition index of 3.5 in June and this dropped to 3.1 in August for 26 individual asessed. Six females with an index of 2.5, were lactating.
In the wet season, adult males generally had condition indices of 4 and 5, but those of the adult females was never as high as 5.

5.3.3 Water requirements and drinking habits

Drinking frequency - Roan antelope came to drink every second day on average in the dry season. During the 72 hour count an average of 1.6 was determined from observations of marked animals (Table 27).
The 1989 count is an anomaly, in that only 54% of the tagged roan known to be in the population were recorded, while only 138 out of an expected population of 150 were counted.

Behaviour - Most roan visited the water during the middle of the day (Figure 21). Data was obtained during waterhole counts in August 1986 and 1987 and September 1984, when a total of 1268 roan came to the waterholes. Even in October, with ambient temperatures of 34°C in the shade, breeding groups came to the water during midday. Animals coming to drink at night included both males and females.
Males spent on average 18.7 ± 24.4 minutes at the water (range 1 - 191 min, n= 74), and females 16.0 ± 14.0 min (range 4 - 43, n = 45). Subadults fell into the same range. These figures were collected during the August waterhole counts in 1988, 1989 and 1991. During the June 1988 waterhole count, four breeding groups of altogether 15 roan approached the water seperately, spent between 188 and 126 min there and left together.
The dominant male at a waterhole was observed to come to the water, interacting socially with other roan and leaving without drinking, but usually defaecating at a particular spot nearby (see also Chapter 6).
Roan stood high in the species hierachy at the water, they were clearly dominant over kudu and warthog, most gemsbuck and sable. Eland drank mostly at night, as did the rhino, so that although these species were dominant over roan, there was little overlap. No interactions between roan and buffalo were observed.

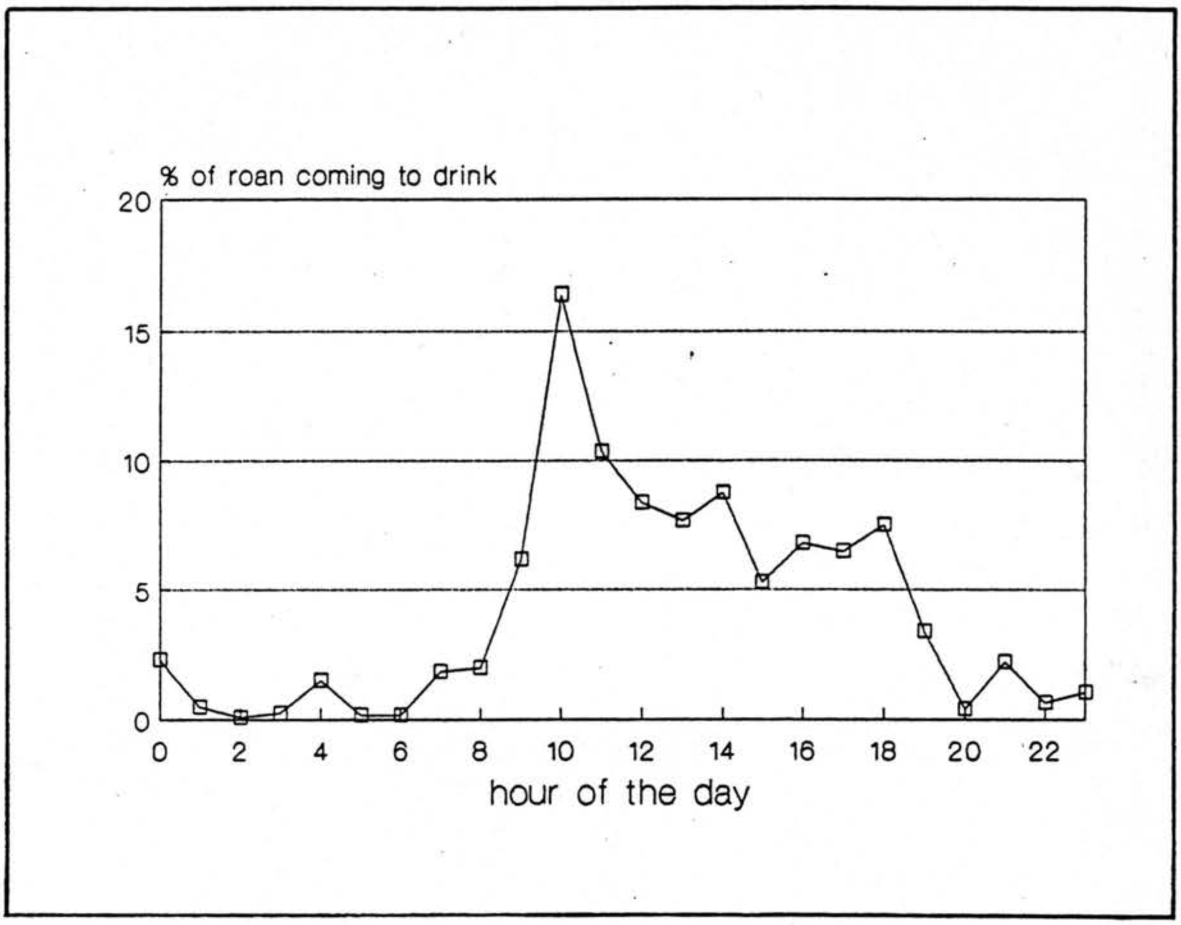


Figure 21: Distribution of drinking times of roan antelope.

Table 24
Faecal nutrient concentrations of captive and free-ranging roan

		nutrient concentrations (% DM) P			Ca			Prot		
Boma	avg±std	0.39 ± 0.11			2.43 ± 0.32			10.03 ± 2.12		
	min	0.26 – 0.56			1.75 – 2.79			7.09 –13.65		
	n	b[1]	6	B	c	6	C	b	6	B
Free-ranging										
Feb./	avg±std	0.39 ± 0.08			1.05 ± 0.42			10.71 ± 2.22		
March	range	0.30 – 0.54			0.44 – 1.64			8.05 –13.61		
	n	b	7	B	b	7	B	bc	7	BC
July/	avg±std	0.22 ± 0.06			0.70 ± 0.26			7.18 ± 0.94		
Sept.	range	0.16 – 0.36			0.36 – 1.12			6.20 – 9.05		
	n	a	10	A	a	10	A	a	9	A
October	avg±std	0.27 ± 0.06			0.45 ± 0.14			12.51 ± 1.70		
	range	0.09 – 0.41			0.13 – 0.76			7.99 –15.56		
	n	a	20	A	a	20	A	c	20	C

[1] as for Table 24

Table 25
Blood and serum trace mineral concentrations for 20 roan marked in October 1987

		Blood (µg/kg) Se			Serum (ppm) Cu	Zn
Ad.males	avg±std	34.50 ± 8.66			1.30 ± 0.33	1.65 ± 0.42
	range	23 – 54			0.8 – 1.8	1.2 – 2.4
	n	b[1]	8	A	8	8
Ad.female	avg±std	20.83 ± 3.53			1.47 ± 0.19	1.60 ± 0.36
	range	15 – 26			1.2 – 1.8	1.2 – 2.0
	n	a	6	A	6	5
Subadults	avg±std	24.33 ± 8.03			1.47 ± 0.15	1.30 ± 0.33
	range	12 – 34			1.2 – 1.6	0.8 – 1.6
	n	a	6	A	6	4
Overall	avg±std	27.35 ± 9.44			1.40 ± 0.26	1.55 ± 0.41
	range	12 – 54			0.8 – 1.8	0.8 – 2.4
	n		20		20	17

[1] as for Table 24

Table 26
Serum concentrations of some trace elements and minerals for roan caught in July 1988

		(ppm) Serum			(mg/l)	
		Cu	Zn	Ca	P	
Ad.males	Avg	1.49	2.00	81.02	19.55	
	Std	0.15	0.89	7.79	3.24	
	min	1.2	1.2	70.14	15.82	
	max	1.6	3.6	96.19	23.73	
	n	7	6	7	AB[1] 3	ab
Ad.female	Avg	1.35	1.78	71.56	16.87	
	Std	0.12	1.06	14.42	1.98	
	min	1.2	0.8	46.89	13.18	
	max	1.6	4.8	88.18	18.45	
	n	13	11	13	A 5	a
Subadults	Avg	1.51	2.08	73.38	26.03	
	Std	0.18	0.59	14.32	1.65	
	min	1.2	1.2	46.89	24.38	
	max	1.8	3.2	96.19	27.68	
	n	11	10	11	B 2	b

[1] as for Table 24

Table 27

Drinking frequencies for roan antelope during the August waterhole counts

Year	Drinking frequency of tagged animals	Estimated drinking frequency of the population
1988	1.6 times	1.7 times
1989	0.54	---
1990	1.6	1.8
1991	1.6	2.0

5.4. Nutrient budgets

In this section preliminary nutrient budgets for protein, phosphorus and calcium are formulated, in an attempt to identify possible deficienies. A distinction is made between values generally considered applicable for roan, here termed potential, and values corrected for local conditions - realized values.

Dry matter intake and dry matter digestibility are interrelated and perceived as the determinant factors in this analysis. They are influenced by foraging time and food abundance on the one hand and nutrients present in the forage on the other (Figure 22).

Dry matter intake (DMI) and diet digestibility - Dry matter intake by grazing ruminants is more closely related to food quality than to animal requirements (Stanley-Price 1977). Food quality determines passage rate and thus, through rumen fill, ingestion rate. A succulent diet, rich in crude protein and low in structural tissue components is easily digested. Renecker & Hudson (1985) working with moose found that diet digestibility was significantly related to diet dry matter, neutral detergent fiber and crude protein content.

Owen-Smith (1988) provides an equation based on the daily food intake (DFI), expressed as dry mass as % of livemass. For 15 herbivores ranging in size from a dikdik to an elephant, $DFI = 6.0 M^{-0.191}$ (SE(b) = 0.039, $R^2 = 0.647$, N = 15, $P < 0.01$). Making use of this regression equation, the dry matter intake for a 250 kg roan would be 5.2 kg per day.

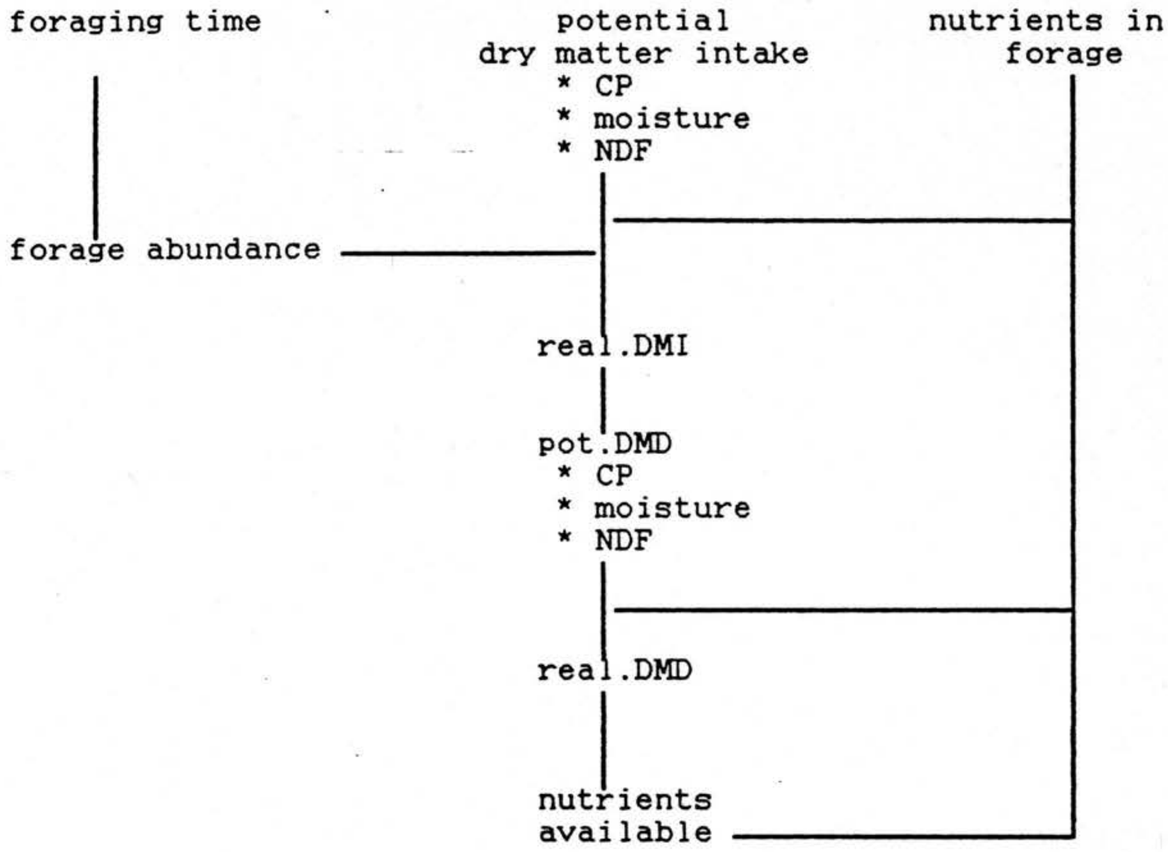
Daily foraging time budget - Foraging is only one of several activities antelopes engage in daily. Time needed to move between feeding area and the water can influence the foraging time available. Owen-Smith (1988) gives a regression line for ruminant foraging time budgets as FB (% of 24 h) = $27.9 M^{0.08}$ (SE (b) = 0.026, $R^2 = 0.46$, N = 12, P = 0.0076).

A 250 kg roan would thus forage for approximately 10½ hours daily or for 126 five minute intervals. Five minute intervals are used for the comparison with grass quantity index in section 5.3.2.2. and Table 22.

Foraging- as opposed to feeding time includes moving while feeding.

Figure 22

The foraging model - the interrelationships



CP - crude protein
NDF - neutral detergent fiber
DMI - dry matter intake
DMD - dry matter digestibility
real. - realized as opposed to
pot. - potential

Table 28
Summary of equations used in formulating nutrient budgets

Dry matter intake for different ruminants under different conditions

cattle	69–104 g/kg $W^{0.73}$	Berry & Louw (1982a)
moose	37–128 g/kg $W^{0.75}$	Renecker & Hudson (1985)
hartebeest	26–87 g/kg $W^{0.73}$	Stanley-Price (1977)
blesbok	84 g/kg $W^{0.73}$	du Plessis (1972)

Relationship between faecal nitrogen (x) and dry matter intake (y) for ruminants

equation 1

DMI = 109.46 FN − 61.89 — for hartebeest
($r=0.681$, $P<0.001$, d.f. 28) — Stanley Price (1977)
DMI = 69.5 if FN = 1.2

Relationship between grass moisture (GM) and dry matter intake (DMI) for ruminants

equation 2

DMI = 2.733 GM − 10.91 — for hartebeest
($r=0.892$, $P<0.001$, d.f.29) — Stanley Price (1977)

Relationships between faecal nitrogen (y) and crude protein % of the diet (x) for ruminants

equation 3

FN = 0.5886 + 0.1492 DCP — for sable antelope
FN = 2.08% if DCP = 10% — Grobler (1981)

equation 4

DCP = 1.75 FCP − 7.75 — for cattle
FN = 1.62% if DCP = 10% — Zimmerman (1980)

equation 5

DCP = 1.677 FCP − 6.93 — for cattle
FN = 1.62% if DCP = 10% — Sinclair (1974b)

Relationships between digestibility coefficient (y) and % crude protein of the diet (x) for ruminants

equation 6

$y = 70 \log x - 15$ — Glover & Duthie (1958
y = 55% if x = 10% — in Grobler 1981)

equation 7

$y = 100.89 \log x - 44.45$ — Bredon, Harker & Marshall
y = 56.4% if x = 10% — (1963 in Sinclair 1974b)

<u>Potential forage intake rate</u> - Forage intake rate is that amount that an animal can find and potentially ingest per unit time. Bite size, forage density and patchiness influence forage intake rate.
Potential forage intake expressed in g/5 min and based on an assumed daily consumption of 7.0 kg for the wet and 3.6 kg for the dry season (see this page for calculation) should exceed 56g and 29g dry mass respectively, to satisfy potential dry matter intake in the foraging time span allocated.

<u>Calculated nutrient intake</u> - The dry matter intake for a standard 250 kg roan is calculated using equation 1, predicting DMI based on the known faecal nitrogen concentrations ([FN]). [FN] for the wet season was taken as 10.7 ± 2.40% faecal crude protein divided by 6.25 and for the dry season as 7.2 ± 0.99% divided by 6.25 (Table 24). Using equation 1, the predicted DMI would be 7.0 ± 2.37 kg in the wet season and 3.6 ± 0.98 kg in the dry season.
To permit this intake (equation 2, Table 28), mean ± one S.E., grass moisture would have to be in the 34.5% to 65.3% range or more, in the wet season and 21.1% to 33.8% in the dry season.
The dietary crude protein content was calculated using equations 3-5. Average values obtained ranged between 7.5% to 11.0% in the wet season and 3.8% and 5.1% in the dry season (Table 29) and compare favourably with actual values determined (Table 23).
Dry matter digestibility was estimated using equations 6 and 7. Values obtained were 33.9% and 26.1% for 5% dietary crude protein (DCP), 55.0% and 56.4% for 10% DCP and 67.3% and 74.2% for 15% DCP.
Protein requirements for maintenance are the sum of metabolic faecal nitrogen and endogenous urinary nitrogen losses. Metabolic faecal protein was taken as 35g per kg DM consumed and endogenous urinary protein as 6.25 x 0.16 x $M^{0.75}$ g/day (Owen-Smith & Cooper 1989).
Phosphorus maintenance requirements were taken as 16 mg/kg livemass. Requirements for growth are 5g per kg of livemass gain (Owen-Smith & Cooper 1989).
The Ca requirements are based on those of growing beef cattle (McDowell <u>et al</u>. 1984).
The availability, intake and requirements for these nutrients are summarized in Table 30.

Table 29
Predicted dietary crude protein content based on faecal crude protein (using equations 3-5)

	wet season	dry season
Grobler (1981)	7.5 ± 2.6%	3.8 ± 1.1%
Zimmerman (1980)	11.0 ± 4.2%	4.8 ± 1.7%
Sinclair (1974b)	11.0 ± 4.0%	5.1 ± 1.7%

Table 30
Nutrient availability, intake and requirements
(on a daily basis)

		Crude Protein	P	Ca
Wet season				
grass concentrations				
January	%	17.8	0.15	0.32
March	%	8.8	0.09	0.59
average for wet season	%	13.3	0.12	0.46
intake (7.0 kg DM)	g	931	8.4	32.2
digested 70%	g	652	5.9	22.5
" 55%	g	512	4.6	17.7
maintenance requirement	g	308	4.0	12.6-72.8[1]
Dry season				
grass concentration in August	%	2.7	0.029	0.241
intake (3.6 kg DM)	g	97.2	1.05	8.68
digested 55%	g	53.5	0.58	4.77
" 30%	g	29.2	0.32	2.60
maintenance requirement	g	188.9	4.0	---

[1] based on the requirement of growing beef cattle

5.5. Discussion

5.5.1 Feeding behaviour - Roan were only observed to graze and not to browse in the wet season.ng observed, in the wet season. As the grasses dried and also in the late dry season, when the browse species started to become green again, the animals were seen browsing. This observation is in agreement with those recorded elsewhere (Joubert 1976, Wilson 1975).

Grass species selection - As pointed out in Chapter 2, roan are adapted to grazing in a medium to tall grass sward. In this study roan selected palatable grasses with a high leaf accessibility. These are grasses with a high leaf to stem ratio, high leaf percentage and which are non stemmy. As in other studies (Wilson 1975, Joubert 1976) a few palatable and readily available species formed the bulk of the diet during any one season. In the wet season when it was green and had a high leaf density, Digitaria seriata was the principal forage species. It became less important as it became stemmy and dried out faster than the other grasses. In the Kruger National Park Themeda triandra and Digitaria pentzii formed 87.4% of the recorded diet in March-April (Joubert 1976). Digitaria pentzii was only eaten occasionally by sable in Zimababwe and roan in Percy Fyfe, despite being dominant in the latter reserve.

Feeding height depended on the accessibility of the leaves. In grasses that are relatively coarse and stemmy at the base, feeding height was much higher, on average 20-26 cm, than in a finer tufted grass such as Triraphis, where feeding height averaged 8 cm.

Brachiaria nigropedata and Eragrostis jeffreysii were utilized by sable antelope on a year round basis in Zimbabwe. Brachiaria was most preferred and also formed the principle food species (Grobler 1974, 1981). Brachiaria was also a very important part of the diet for sable antelope on Percy Fyfe nature reserve (Wilson 1975).

Like sable in Zimababwe, where 10% of the available grass tufts were utilized, roan in this study utilized 13% of the tufts available while on Percy Fyfe 15% of the available grasses were taken (Wilson 1975, Grobler 1981). This indicates a similar selectivity.

Browse species selection - Roan browsed on four species Grewia reticulata, Lonchocarpus nelsii, Acacia ataxacantha and Ochna pulchra.

Four browse species were also utilized by sable in Zimbabwe, _Grewia flava_ being one of them (Grobler 1974). _Acacia spp._ were sought after by roan on Percy Fyfe and browsing on _Lonchocarpus capassa_ was noted for roan in the Kruger N.P. by Joubert (1976). _Ochna pulchra_, generally considered unpalatable (Owen-Smith & Cooper 1987), was eaten when new leaves were formed.

5.5.2 The availability of key nutrients to the roan

5.5.2.1 Soil nutrient concentrations - Average values of all four minerals are well below the range recorded for different sable and roan habitats in the Transvaal and Zimbabwe (Wilson 1975). Even maximum values recorded on the plateau are below those recorded elsewhere, apart from Ca (0.065%) (Table 31). It is thus apparent that the sand is highly leached.

5.5.2.2 Availibilty in the forage - **Grass biomass** Jankowitz & van Rensburg (1985) measured grass biomass in the four major vegetation types on the plateau during 1980 by clipping quadrants (Table 21). Their results compare favourably with those from this study.
That grass quantity is no limiting factor is also apparent from Table 22 and the projected daily dry matter intake rates of a 250 kg roan: 56 g in the wet season and 29 g in the dry season per 5 min of foraging.

Grass nutrient content - The crude protein levels compare well with values obtained in the study by Rutherford (1975) on an ungrazed section of the Waterberg. They also correspond to crude protein concentrations obtained for Natal sour sandveld (O'Reagain & Mentis 1988).
While the protein content is more than sufficient in the wet season, it drops below maintenance requirements of about 5% (Sinclair 1974b) in the dry season (Table 23). This deficiency also shows up in the protein budget.
The higher protein level in the rocky areas and drainage line can be explained by the data in Table 32. The rocky areas have a higher soil nutrient content and with it a higher crude protein content. Although no fibre analyses were carried out to prove this, the advantage of the significantly higher crude protein content probably outweighs the disadvantage of a higher crude fiber content in the wet season, but not in the dry season. Roan thus select areas with a high soil nutrient content in the wet

season and move to the more sandy areas in the dry season with a more favourable crude protein to crude fiber ratio. Heitkönig (1987) made a similar observation on habitat selection by roan antelope on Nylsvley.
Grasses have normal levels of 0.2–0.5% P and 0.3–0.6% Ca on a dry matter basis (Bransby 1981). In the Matopos, Zimbabwe, Grobler (1981) recorded 0.34% P (SE 0.07, n=103) and 0.33% Ca (SE 0.17, n=97) in sable habitat. Values for 58 grasses grown on the same soil in Kenya were P 0.05–0.37% and Ca 0.09–0.55 (McDowell et al. 1984).
The wet season Ca levels of grass determined in this study compare favourably with normal values. P levels however, although they compare well with those reported by Walter & Volk (1954), by Rutherford (1975) for the Waterberg and by Kruger (1988) for different species growing on Kalahari sand, are significantly lower.
The average Ca:P ratios are favourable early in the wet season, but become wider as the dry season progresses, e.g. 10.2 ±6.4 : 1 in August. A 2:1 ratio is considered desirable.

5.5.2.3 Nutrient status of roan

Faecal nitrogen (FN) has been shown to be positively correlated with dry matter intake, dietary digestibility, dietary protein and ruminal N. FN content represents a combination of unabsorbed DN, undigested microbial N and endogenous N (Leslie & Starkey 1987).
FN alone provides a viable index of diet quality which may be used to compare: 1) seasonal changes experienced by a single population (assuming no radical changes in the consumption of secondary compounds), 2) year to year changes in a given season (assuming no radical changes in forage availability, which affect diet selection), and 3) within-season variations affecting disjunct populations that occupy similar habitats and are therefore likely to consume similar diets. (Leslie & Starkey 1985, Stanley Price 1977, Renecker & Hudson 1985, Mould & Robbins 1981).
Phenolics in the forage tend to elevate the FN content (McLeod 1974, Mould & Robbins 1981).
Observed faecal crude protein values ranged between 6.21% and 14.34%. Seasonal means follow the expected pattern, with a sharp rise in October attributable to the green flush of grass and browse after the first rains.
Gates and Hudson (1981) found that weight loss of Rocky Mountain elk was associated with a FN content below about 1.6% (10% protein).

Table 31
Mineral content of sand on the plateau as determined by Jankowitz (1983) compared to the expected range (Moen 1973) and values recorded by Wilson (1975) for various sable habitats.

	all values as %		
	Jankowitz	Moen	Wilson
Phosphate	0.0008	0.01–0.20	0.04–0.29
Potassium	0.003	0.17–3.30	0.22–2.50
Calcium	0.0077	0.07–3.60	0.05–1.50
Magnesium	0.0018	0.12–1.50	0.05–0.34

Table 32
The characteristics of dunes and valleys in Kalahari or Miombo sandveld (adapted from Bell 1981)

	Dunes	Valleys
soil type	sandy	clayey
nutrient status	low	high
infiltration rate	high	low
woody production	high	low
grass production	low	high
grass quality		
crude protein CP	low	high
crude fiber CF	low	high
CP/CF	high	low

Calcium levels in the blood are under hormonal control, but those of faeces, liver and milk are positively related to intake.

Faecal Ca - The mean value for roan fed lucerne containing 2.4% Ca is nearly identical to the normal value for cattle and to the 2.5% Ca recorded for wildebeest in Etosha (Berry & Louw 1982). However the July mean for free ranging roan dropped to 0.70% and only rose to 1.28% during December. These levels are lower than those recorded for cattle from the same geological formation, which are already considered low (Table 33).

The very low value (0.45%) for the 20 roan marked in October 1987 is considered to be an artefact of incorrect analysis (Grant 1989 pers.com.). Faecal Ca follows seasonal fluctuations in forage Ca in a predictable pattern.

Differences between adult males and adult females plus subadults were significant for the 1987 sample, but not for that collected in 1988/89.

Serum Ca is just below the level of 80 mg/l, which is considered normal (McDowell et al. 1984).

Phosphate Blood phosphate levels are related to those in soil and vegetation but milk P stays fairly constant (Wilson 1975). Faecal P is directly related to dietary P intake (Leslie & Starkey 1985).

Normal plasma values for cattle are from 4-6 mg/100 ml (adults) to 6-8 mg/100 ml (subadults) (Church 1979, Engels 1981). Although faecal P in roan compares well with values considered normal for cattle and wildebeest (0.30% DM), the serum concentrations are less than 50% of the critical level (Table 26). This might in part be ascribed to the fact that the serum was collected from captured roan. The P level decreases significantly in stressed animals, this has been observed for waterbuck, impala, wildebeest and eland, but not for big horn sheep (Drevemo et al. 1974, Engels 1981, Franzman 1972, Melton & Melton 1982 and Seal et al. 1972).

The discrepancy between low serum P, and faecal values which seem normal, may be partly due to the wide Ca:P ratio in the dry season, when the samples were collected. Rickets & Weinmann (1970 in Grant, 1989) found that the wider the Ca : P ratio, the more P is excreted in the faeces. This would explain the seemingly adequate faecal concentrations in roan since the Ca:P ratio is wide and forage contains very little P.

Of several blood parameters tested in a large sample of Alaskan moose, only the mean phosphorus content was

Table 33
Mineral concentrations in cattle (Grant 1989) and roan antelope (this study) occupying similar habitats

Habitat characteristic	Cattle mean	Cattle status	Roan mean
Geology (Etjo formation)			
faecal calcium (g/kg)	12.8	low	9.3
faecal phosphate "	2.74	low	3.1
Soil (Cambic Arenosol)[1]			
liver cobalt (mg/kg)	0.26	medium	
liver copper "	166	high	425
liver iron "	221.1	medium	348
liver manganese "	10.2	high	11
faecal calcium (g/kg)	15.3	medium	9.3
faecal phoshate "	2.88	low	3.1
milk iodine (μg/l)	115.8	high	
Vegetation (Northern Kalahari)			
liver manganese (mg/kg)	9.4	low	11
liver iron "	224.9	low	348
faecal calcium (g/kg)	14.2	low	9.3
faecal phosphate "	2.68	low	3.1
milk iodine (μg/l)	85.5	low	
Relatively homogeneous production areas (Waterberg sand)			
liver zinc (mg/kg)	136.4	medium	215

[1]FAO soil classification

significantly lower in lactating than in non-lactating females (Franzmann & LeResche 1978). The serum P levels of adult female roan were non-significantly lower than those of males.
Phosphorus levels increase with improved body condition in Alaskan moose (Franzmann & LeResche 1978), big horn sheep (Franzmann 1972) and sable antelope (Wilson 1975). Adult moose in average or better condition should have a P blood level of 5.2 mg/100 ml or more. Mean values for big horn sheep from different populations lie between 4.4-5.8 mg/100 ml and for sable between 5-14.4 mg/100 ml. The average value for four waterbuck recorded in the Umfolozi Game Reserve was 6.1 mg/100 ml (Melton & Melton 1982). Significant differences ($P<0.05$) in plasma P were recorded between seasons, sexes and adults vs. immatures for wildebeest (Berry & Louw 1982a). In the present study subadults had a significantly higher serum P concentration than adult females, with that of adult males intermediate (Table 26).

Trace minerals Concentrations of those trace minerals examined seem to be adequate. Sodium was not investigated but is probably deficient. When deprived of rock salt blocks, game was commonly seen to eat soil from a gravel road, brought onto the plateau. Salt licks were used by all the game species. The liver copper, iron, manganese and zinc values are all medium to high for the two samples analysed. The liver copper concentration is very high but still well below the toxic level of 700mg/kg (McDowell et al. 1984). Blood selenium levels do not indicate any deficiency.

Deficiency symptoms The phosphorus content in the forage should be 0.18-0.70% of the dry matter intake for beef cattle. Scrivner (et al. 1988) recommend that it should be 0.25-0.27% for black-tailed deer. Important differences exist between different animal breeds and species in their capability to absorb minerals from the diet. For example 5-35% of the Mg, 40-80% of the P and 2-10% of the Cu in the diet was absorbed in one comparison of different ruminants (McDowell et al. 1984, Church 1979).
Grazing cattle were more prone to develop P deficiencies, and the clinical signs are severest, after the rains, when pastures are green and plentiful. This is the time when the animals are actively growing and their P demands are greatest (McDowell et al. 1984).

Feed intake is depressed if the forage is P deficient. This seems to be related to decreased microbial digestion caused by the limited availability of P in the rumen.
Body mass is also affected. A difference of 121 kg between supplemented and unsupplemented cattle has been recorded at Armoedsvlakte, a P deficient area. Mortality rates were also higher for P deficient animals. Cumulative mortality rates for the two groups of cattle over 5½ years were 27.3 and 58.3 % respectively.
Conception rates, calving and weaning percentages are depressed. Birth and weaning mass, as well as average daily gain from birth to weaning is lower for P deficient cattle (Read, Engels & Smith 1986b). Similar results have been recorded by McDowell et al. (1984).
Botulism (lamsiekte) and aphosphorosis (stywesiekte) occurs in P-deficient areas. Botulism is caused by the toxin secreted by Clostridium botulinum in decaying carcasses. The toxin paralyses the musculature when animals chew infected bones. Pica, or more specificically osteophagia, is a P-deficiency symptom commonly observed on the plateau.

Visual condition index This index is not an accurate indication of the animals'true physiological condition (Monro & Skinner 1979). However it is apparent from the data, that roan loose condition in the dry season and that reproducing adult females are generally in the worst condition.

5.5.3 Water requirements and drinking behaviour **Drinking frequency** In this study roan came to drink on average every second day during the dry season. In the Kruger N.P. roan drank daily during the dry season (Joubert 1971, 1974a). Kingdon (1974) states that roan drink regularly and in great quantity, sometimes visiting a waterhole twice a day, but that they can go without water every second day during the dry season.
Drinking time In this study it was observed that 87.5% of all roan came to drink during daylight hours and 64% between $10.^{oo}$ and $17.^{oo}$ h. Joubert (1971) observed that roan in Kruger N.P. would normally drink between $10.^{oo}$ and $11.^{oo}$h, but in this study only 16% drank during this time.

Chapter 6: Sociology, behaviour and space utilization

6.1. Introduction: In this chapter the social organization and use of space by roan antelope is discussed as these two ecological attributes are interrelated (eg. Jarman 1974).

Four different social systems are recognized among bovids, namely a) solitary/territorial, b) solitary/non-territorial, c) gregarious/territorial and d) gregarious/non-territorial. Of the 70 bovids in Sub-Saharan Africa, 41 species are gregarious and all but about 10 are territorial (Estes 1974).

Three social classes are universal in the gregarious antelope: breeding or nursery groups, bachelor groups and solitary adult males.

Clans (also known as subpopulations or population units) have been identified for several larger herbivore species. A clan, the term used here, comprises unstable breeding groups that share a home range. The breeding groups of a clan exchange members and thus their composition is variable. Exchange between clans takes place mainly by dispersing subadult males. Examples are elephant (Smuts 1974), black rhino (Joubert & Eloff 1971, Mukinya 1973), buffalo (Brooks 1982), plains zebra and blue wildebeest (Smuts 1974 and Brooks 1982) and impala (Smuts 1974 and Murray 1982).

It is generally agreed that a territory is a geographically fixed spatial area. Three related concepts, defence, exclusion and dominance receive variable emphasis, depending on the definition used. Only approximately one-third to two-thirds of the adult males in a population are territorial during the breeding season. Species occupying savanna usually have boundary orientated territories, where scent marking is usually a prominent feature, as opposed to "stamping grounds" in open grassland where the males are in visual contact most of the time (Owen-Smith 1977).

Home range is a relatively old concept. It was introduced by Hediger (1942/50,1949,1951 in: Leuthold 1977) in Europe and by Burt (1940,1943,1949 in: Leuthold 1977) in America, but is still relatively poorly defined. Different names and definitions are used for the home range and its components, and different methods are employed to calculate it (Anderson 1982, Clark & Gilbert 1982, Don & Rennolls 1983, Dunn & Gipson 1977, Jenrich & Turner 1969, Jewell 1966, Johnson 1980, Metzgar 1972, Samuel & Garton 1987, Van Winkle 1975, Van Winkle et al. 1973 and Voigt & Tinline 1980).

The home range has been variously defined; by Jewell (1966) as the area over which an animal commonly travels in pursuit of its routine activities . Leuthold (1977) defines it as the area that an animal is familiar with and does not leave voluntarily. Anderson's (1982) definition is based upon the bivariate probability density function that gives the likelihood of finding a specific animal at a particular location on a plane. This density function is termed the utilization distribution or occupation density distribution. The home range is then the smallest area enclosing a fixed percentage (such as 95%) of the animal's space utilization.

"The choice of the method is not only guided by the objectives of the study and nature of the data, but also by how the researcher wishes to regard spatial distributions" Don and Rennolls (1983). The objective of this study was to relate home range size and configuration to variables such as group size, sex and age, habitat, time of year and use of the home range over several years.

Roan antelope, together with sable, impala, waterbuck and Lichtenstein's hartebeest are gregarious antelope that inhabit the ecotone between closed woodland or thickets and open savanna, particularly dambos (wide, grass-covered drainage lines in Brachystegia spp. woodland) (Estes 1974, Pienaar 1974 and Joubert 1976). When considering habitat selection, it is important to realise that this selection takes place at different levels, ie. species distribution range (first order selection), home range selection (second order) and special activity area selection (third order), such as feeding areas (Johnson 1980). It is important to recognise that many of the habitat components within an animal's home range are not necessarily suitable, but lie in between those required by the animal to feed, drink and rest in.

6.2. Methods: Observations on group structure were made throughout the study. Groups were identified, where possible using known individuals, and the age and sex composition was noted. Data collected during waterhole counts is not included, unless specifically stated. Clan structure data was collected especially for the "Duinedam Clan", a clan including nine marked individuals moving over the ranges of four marked adult bulls.

Behavioural observations were made opportunistically throughout the study.

Distribution data was collected for 29 individually marked roan in addition to one adult male and four adult females, which were radio-collared (see also Chapter 2).

The location at which an individual animal was first observed on a particular day, was used for home range determination. Radio-tracking was done at different times of the day, so as to cover the different localities used during the daylight hours. No radio-tracking was done at night. This proved impractical as the roan were relatively wild and because of the difficulties of getting good triangulations in the dark.

A 1:50 000 topographical map with an overlying grid was used to record distributional data. Accuracy of fixes was achieved by homing in on the individual animals as far as possible, before taking the triangulation fixes.

Home range is equated with life time range, being the area an individual animal covers during its life. The study period however is only a sample in the life of an average roan. The seasonal range is that area which an animal utilizes during either the dry or wet season. The dry season was taken as lasting from May to the end of October, the remainder of the year being the wet season.

Different methods were used to estimate home range: convex and concave polygon, harmonic mean method and the exponential kernel estimate. For the harmonic mean estimate and the kernel estimate an algorithm developed by Button (1986) was used.

It produced a matrix which was plotted in graph form by using the Statgraphic package.

6.3. Results: **6.3.1. The social units** - Three main social units were recognized, namely breeding groups, consisting of adult females and their offspring, bachelor groups and thirdly solitary males. 543 groups involving 2284 roan antelope were classified (Table 34).

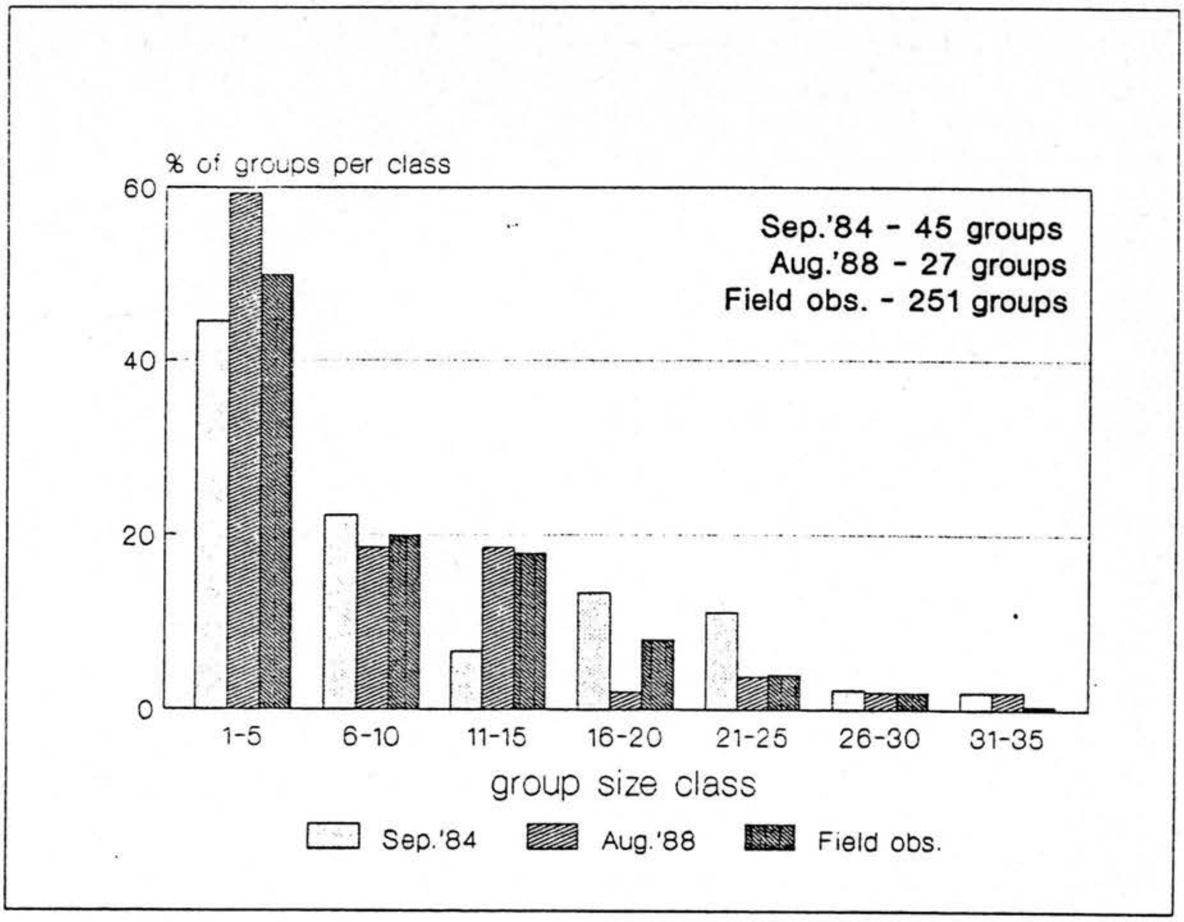
Breeding groups - 38.7% of all groups encountered, were breeding groups. Average group size during the study was 8.5, with a range of 2-32. In addition 24 single females and 7 single subadults were observed. The group size distribution is shown in Figure 23, for three samples, namely the 72 hour waterhole counts in 1984 and 1988 and the breeding group observations during the study (field obs.) away from the water. The two waterhole counts differ significantly from the field observations (chi-square 24.49, 3 d.f P = 0.00002 and chi-square 7.97, 3 d.f. P = 0.047). In 1984 prior to the captures 26.7% of the groups coming to drink had 16 or more members, compared to 3.7% in 1988 (immediately after the captures), and 12.3% for the field observations.

Breeding groups, numbering 5 or fewer individuals, constituted 43% of such groups (Figure 24) and this fraction remained constant throughout the year (chisquare = 4.831, 3 d.f., P = 0.185).

Individuals in the breeding groups sharing a home range and thus being part of a particular clan, never formed a stable herd, but split up into different groups, the composition of which changed constantly. This process is illustrated by the Duinedam clan, which had the most marked animals. In Figure 25 the composition of the clan, is shown by age and sex classes. Individuals were moved into the next age class at the end of the third quarter - the early breeding season. Adult males are not included in this analysis. In Figure 26 the size of this clan is shown together with the average group size and largest group observed per quarter. During the 10 quarters of observation, the largest group observed per quarter averaged 75% of clan size and the average group size per quarter averaged 45% of clan size.

Figure 23: Breeding group size distribution as observed during the September 1984 and August 1988 waterhole counts, as well as throughout the study (Field obs.).

Figure 24: The fraction of breeding groups with less than 6 animals as observed during the different quarters of the year. The number of groups counted and the monthly range are indicated.


% of groups per class
60
40
20
0
Sep.'84 - 45 groups
Aug.'88 - 27 groups
Field obs. - 251 groups
1-5
6-10
11-15
16-20
21-25
26-30
31-35
group size class
Sep.'84
Aug.'88
Field obs.

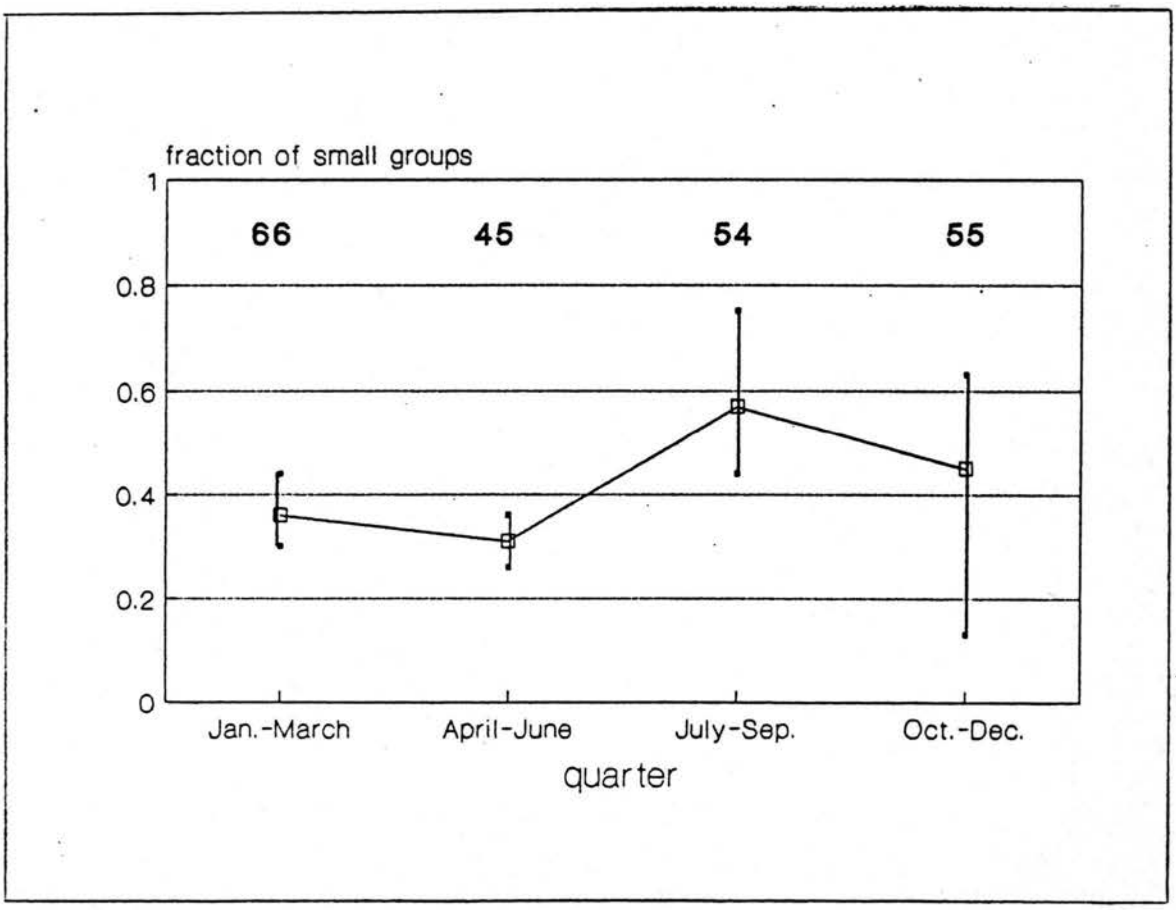
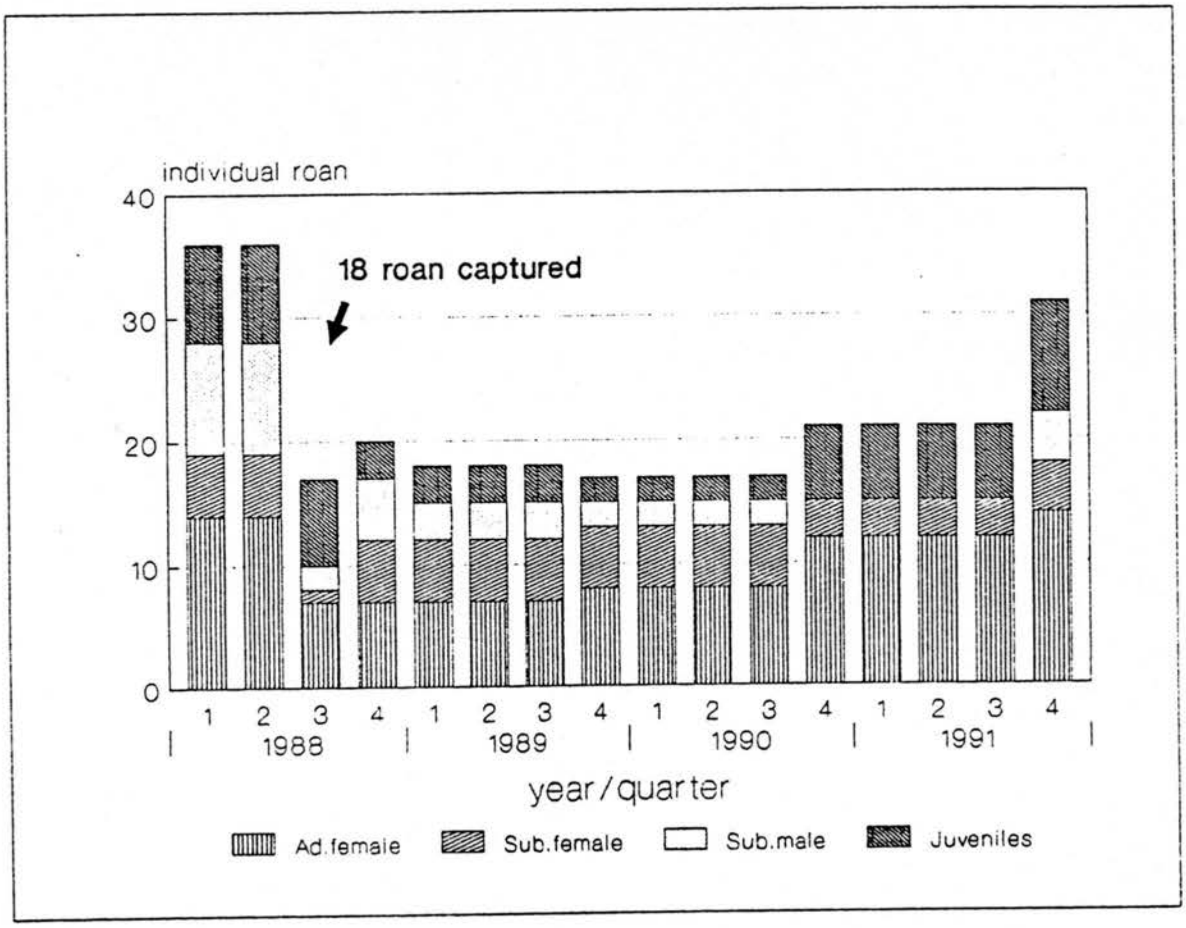
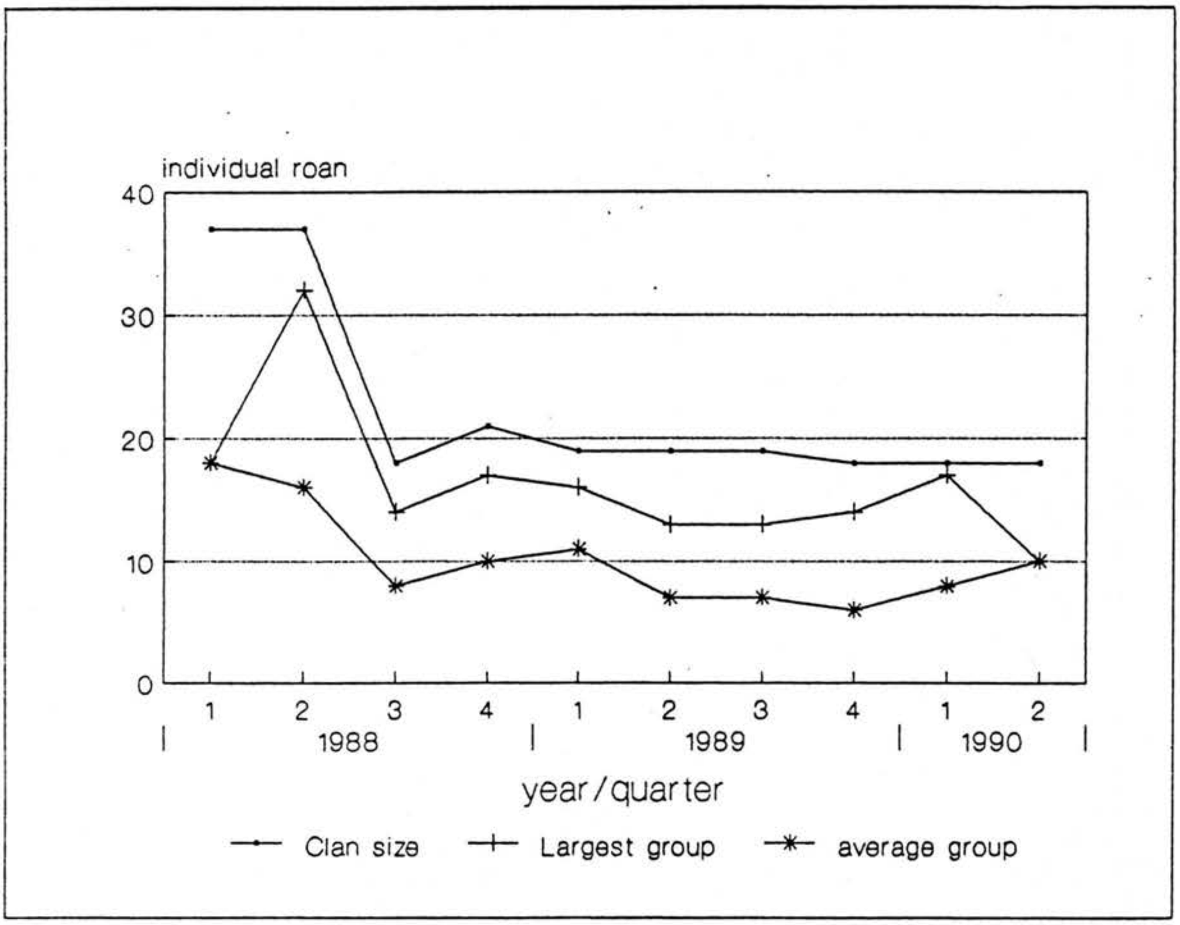

fraction of small groups
1
0.8
0.6
0.4
0.2
0
66
45
54
55
Jan.-March
April-June
July-Sep.
Oct.-Dec.
quarter

Figure 25: The sex/age composition of the Duinedam clan over four years. Sample size and ranges for the individual months per quarter are indicated.

Figure 26: The Duinedam clan size, the largest group observed and the average group size during the different quarters.

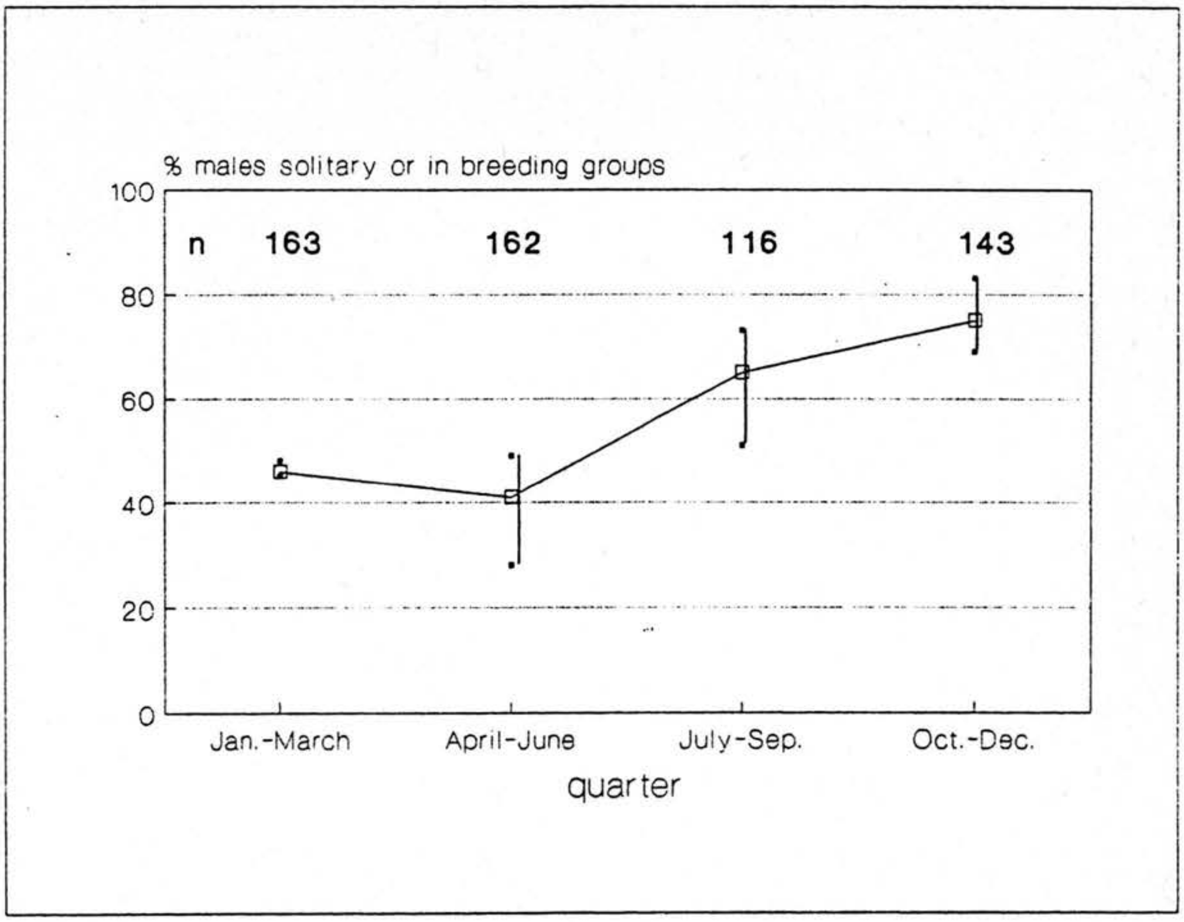

individual roan
18 roan captured
40
30
20
10
0
1 2 3 4 1 2 3 4 1 2 3 4 1 2 3 4
1988 1989 1990 1991
year/quarter
Ad.female
Sub.female
Sub.male
Juveniles

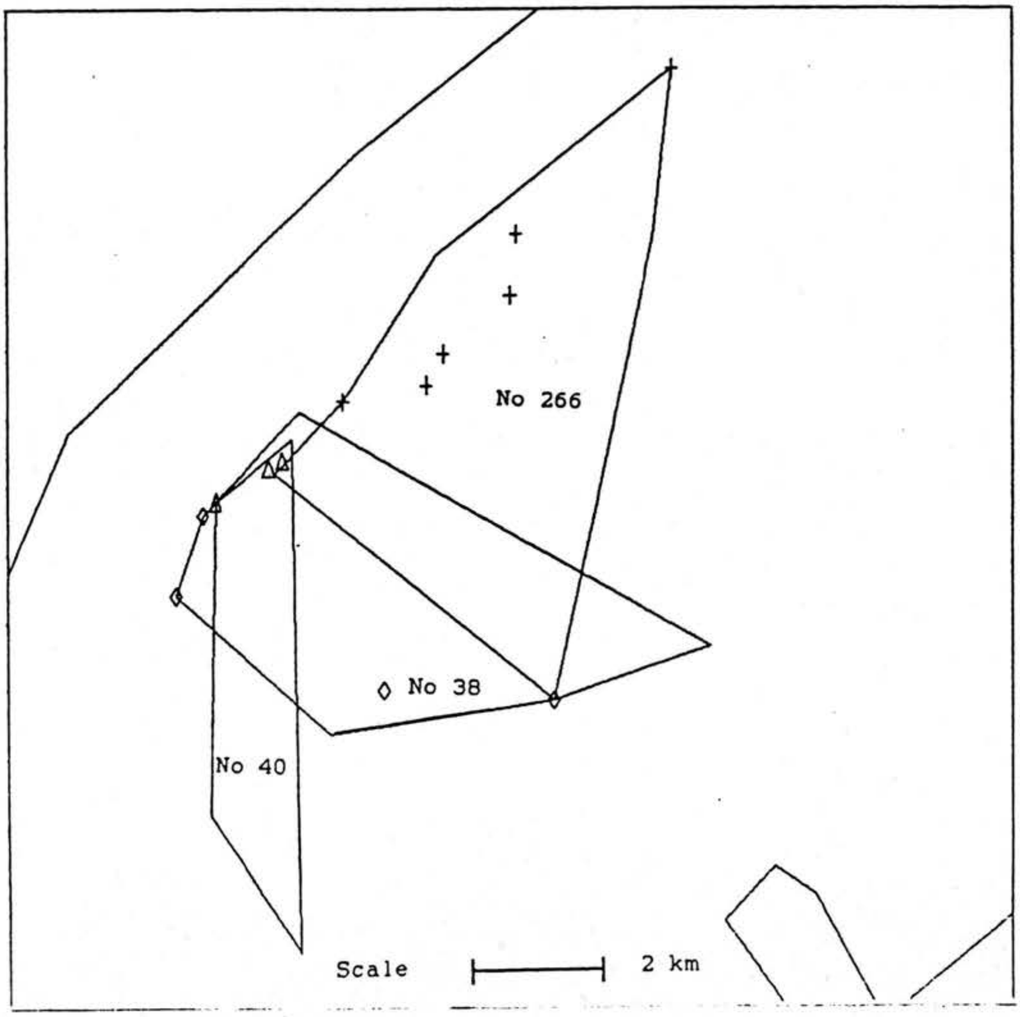

individual roan
40
30
20
10
0
1 2 3 4 1 2 3 4 1 2
1988 1989 1990
year/quarter
Clan size
Largest group
average group

Bachelor groups - 13.1% of all groups were composed of two or more males. Males left the breeding groups when two years old, becoming solitary or joining a bachelor group.
Examples of individual males leaving the breeding group and joining bachelor groups to then become dominant breeding males are illustrated by following three cases.
Male No 20 This young male was seen twice in January 1988, when approximately 2 years old, in a bachelor group. From February until late April he was observed again in his natal breeding group. On at least one occasion a dominant male was also present in the group. From May onwards No. 20, now two-and-half years old, was observed in the company of 1-13 bachelors. In December '88 and in 1989 he was observed three times on his own. In 1990, now 4 years old, he was again in the company of 1 or 2 other males approximately his own age and had moved into the neigbouring clan range. In May and July 1991, now five-and-half years old, he was seen together with breeding groups of four and 16 animals, being the dominant male. In August 1991 he was clearly one of the dominant males at the waterhole.
Male No 24 was eartagged when 18 months old. Between July and December 1988, he stayed in his breeding group. In February 1989, now two years old, he was observed on his own and in July and August again together with his natal group. During 1990 he was observed on his own on three occasions and once in a bachelor group. In 1991, now four years old, he was seen once on his own and on the other occasion in August coming to the water in a breeding group of 24 roan, including a dominant male.
Male No 29 was ear tagged when approximately 4½ years old. During that year he was observed twice on his own and once together with a male, of his own age, in a breeding group. In 1989, when five years old, he was observed in the second half of the year on six occasions as dominant male in a breeding group. In 1991 (7 yrs) he was observed in a bachelor group of five males, clearly being the dominant male. In August he was seen at the water on three occasions, once with a group of juveniles, once on his own and once with another male. His behaviour was still that of a dominant male.
Solitary males - 231 solitary males were observed during the study. The proportion of single males (either solitary or in breeding groups) in relation to all males encountered, was found to differ seasonally (chisquare = 19.54, 3 d.f., $P < 0.001$). From July to December, but especially in the last quarter,

Figure 27: The percentage of males that were observed single or in breeding groups during the study. Sample size (males observed) and the monthly range are indicated.

Figure 28: The home ranges of three adult males. The localities where each male was observed with a breeding group are indicated.


% males solitary or in breeding groups
100
80
60
40
20
0
n
163
162
116
143
Jan.-March
April-June
July-Sep.
Oct.-Dec.
quarter


No 266
No 38
No 40
Scale
2 km

the fraction of single males and those in breeding groups was greater than expected (Figure 27).
Ten individually known adult males, five years and older, were seen on average 61% on their own, in 15% of the sightings in a bachelor group and 24% of the time in breeding groups (Table 35). All males apart from No. 29, with a small sample size, were most frequently seen on their own.

6.3.2. Territorial behaviour

In their wet season home range, the Duinedam breeding groups moved through the territories of at least 4 males, in the 1987/88, 1988/89 and 1989/90 breeding seasons, see Figure 28. The fourth male left his home range in the second breeding season and moved to the home range of a different clan.
Male No. 266 was observed on four occasions with the breeding group, between the 8 December 1988 and 24 January 1989. On the 26 January 1989 the breeding herd was with male No.40, whose territory is adjacent to that of male No. 266.
During the next breeding season, 1989/90, the breeding group was observed on two occasions with male No. 40 and three times together with male No. 38. Although the home ranges of these individual males overlapped considerably, the areas in which they were observed in the company of a breeding group, presumably in their territories, did not overlap (Figure 29).
No individually recognizable male was observed for any length of time in the same breeding group on the plateau.
Patrolling, especially along roads, defecating every 50-100 meter, as described by Estes & Estes (1976) for territorial sable males, was observed in this study by fully adult roan males.
Observations indicate that males abandoned their territories, after the main breeding season, and joined the bachelor groups, as explained in the previous section.

Table 34

Frequency with which the social units were recorded during the study

	n	
Breeding groups		
single adult females	24	4.4%
single subadults (excl. males) and juveniles	7	1.3%
breeding groups with 5 or less members	91	16.8%
breeding groups with more than 5 members	119	21.9%
Bachelor groups	71	13.1%
Solitary males	231	42.5%
Total number of groups	543	100.0%

Table 35

Frequency of different associations formed by individual adult males

Male no.	alone	with ad.males	with ad.females/subad.
266	14		6
40	6		3
38	16		4
31	7		0
30	3		1
29	1	2	6
15	3		1
1	19	17	4
10	6		3
20	4		3
total	79	19	31
average %	61	15	24

6.3.3. The home range size and configuration as influenced by:

a) Method of analysis - For the Duinedam clan, with nine marked individuals, one of which had been radio-collared, 102 locations were collected over a 29 month period. This data set was used to compare the different methods of home range analysis.

The annual home range estimates, at the 95% level, derived from the exponential kernel methods (4235 ha) is considerably smaller than the estimate of 5536 ha, derived using the convex polygon method, whereas the 95% concave polygon estimate is only 3680 ha (Table 36).

The calculated shape of the convex polygon and exponential kernel estimate is shown in Figures 29 and 30.

The harmonic mean home range estimate is shown in Figure 31, which illustrates the unrealistic shape and size estimate of this method.

b) Habitat - With the limited data and the apparent similarity of habitat utilized by the two clans, no habitat influence on home range size could be detected, apart from seasonal effects. In the wet season the Duinedam groups concentrated in a fairly small area of their wet season range, compared to the fairly even use made of theirs by the Elandsdrink groups.

c) Time of year - The Duinedam groups utilised 5921 ha in the wet season (based on all 53 observations), compared to 3498 ha in the dry season. However 81% of the wet season observations lie in a area of only 687 ha, 12% of the wet season range. Thus although this group ranged over a larger area in the wet season, most of the observations are concentrated in a much smaller area than during the dry season (Figure 32).

d) Group size - Adequate sample of location points were obtained for two clans only and these two are compared. The Duinedam breeding group had 36 members in 1988 prior to the capture and the Elandsdrink one 26, 72% the size of the other clan.

The Elandsdrink annual and dry season home range estimates were 74% and 75% the size of the bigger Duinedam clan. The wet season home range size was 57% of that of the larger clan.

e) Sex and age - Four adult females had an average home range of 5272 ha, compared to 4597 ha for three subadult males. The territory of one radio-collared male was estimated to be 1217 ha. This is comparable to the home range size of two adult, mostly solitary females, namely, 1152 and 1780 ha respectively.

f) Long term observation of home range - Home ranges of the breeding groups appear to be very stable. No female was observed to shift its home range during four years of observation. A known female has been observed at the same waterhole for 9 years. Some subadult and adult males shifted their home ranges, both in dispersing from their natal groups and also as mature and dominant males. Out of 3 marked subadult males, one moved into the range of a different clan. Two out of 11 known adult males moved their home range into those of different clans. The radio-collared male wandered widely before changing his range.

Figure 29: The locational points of the Duinedam clan and superimposed the shape of the convex polygon estimate (95%).

The grid is 10 by 10 km

Figure 30: The locational points of the Duinedam clan and superimposed the shape of the exponential kernel estimate (95%).

The grid is 10 by 10 km

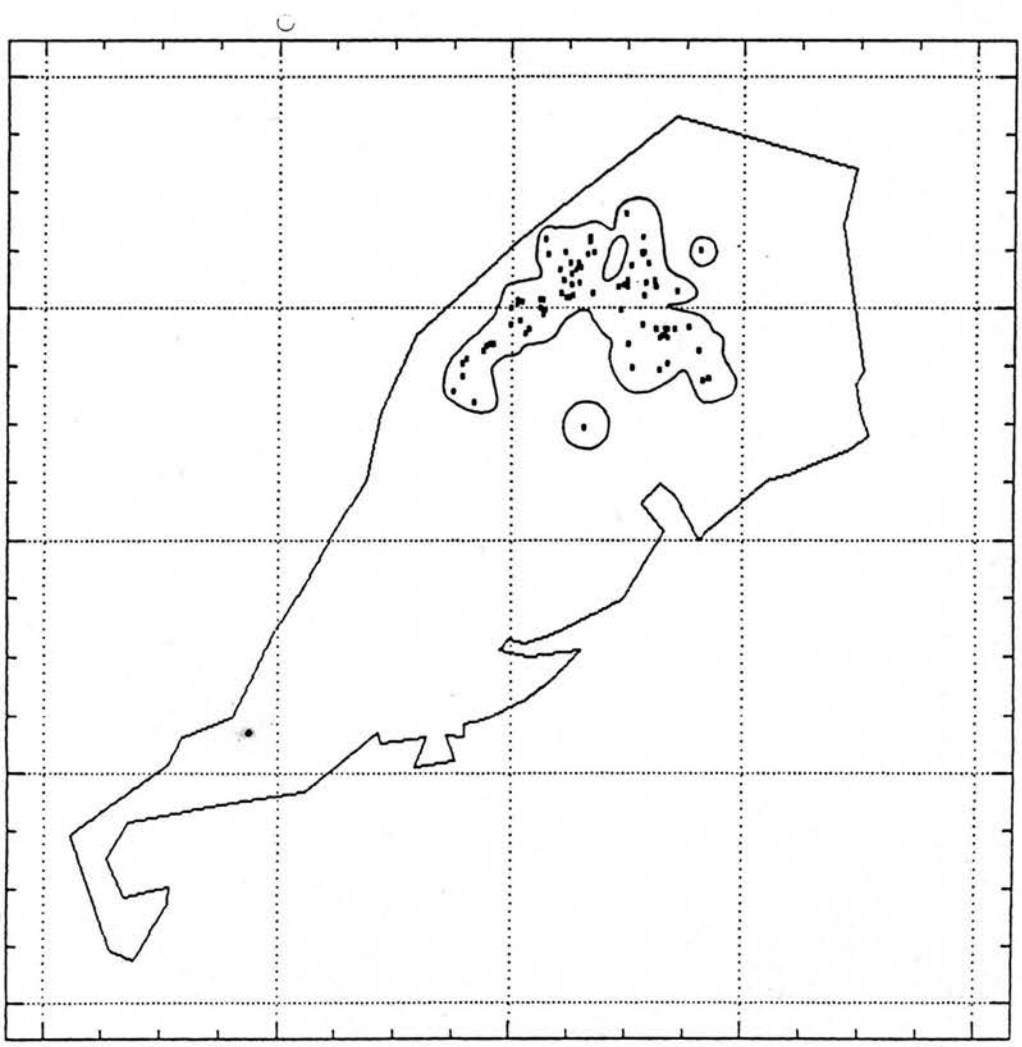


Figure 31: The harmonic mean estimate of the Duinedam home range. The 10, 25 and 50% levels in relation to the recorded localities are indicated.

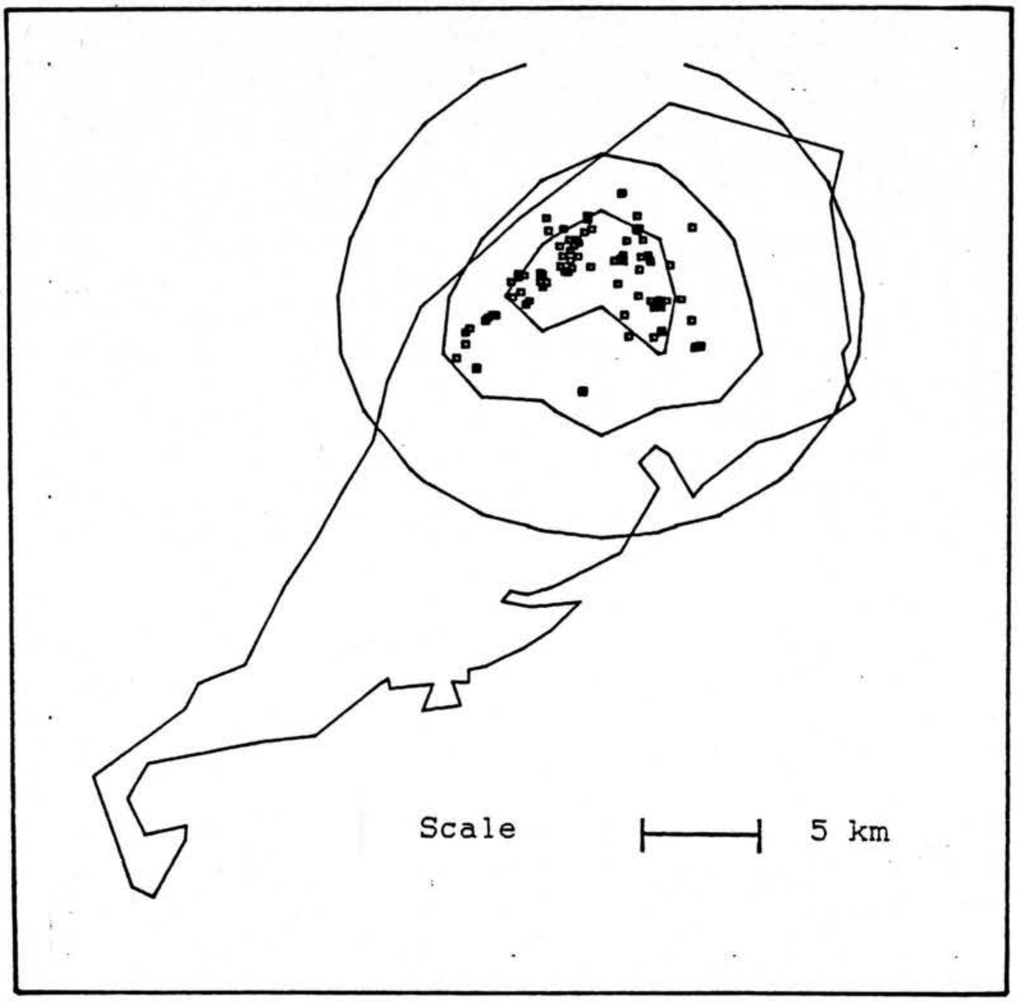
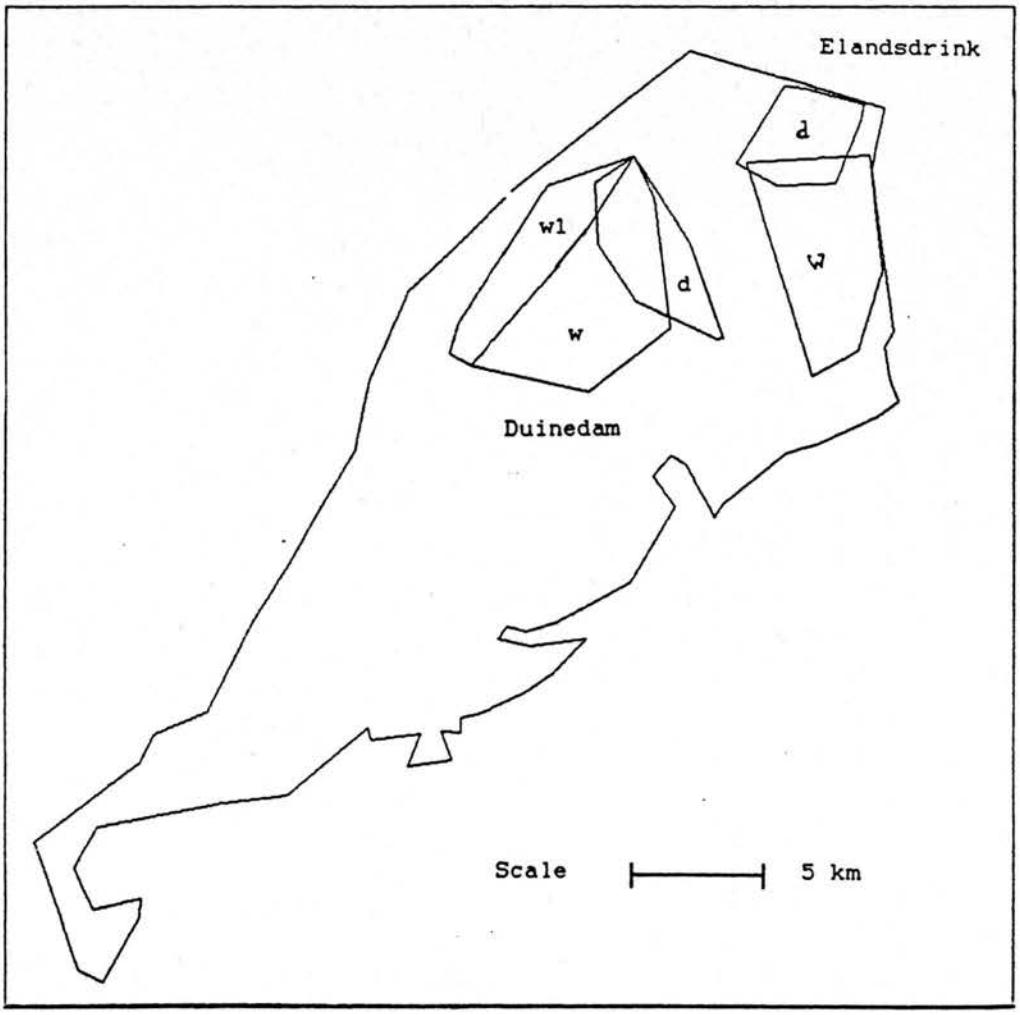

Scale
5 km

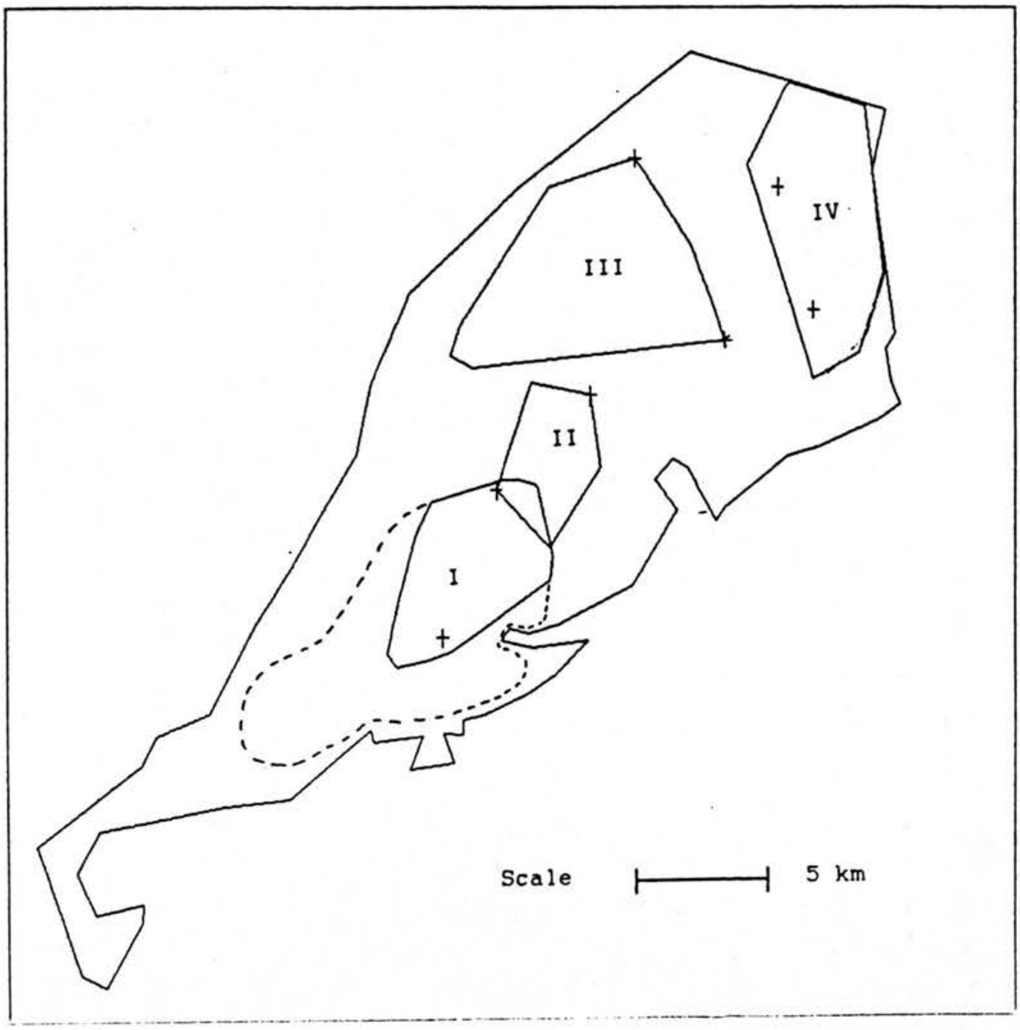
Figure 32: The home ranges of the Duinedam and Elandsdrink clans. The dry (d) and wet (w) season ranges and for the Duinedam group the wet season range (w1) covering 81% of the observations are indicated.

Figure 33: The home ranges of the different clans. The Geelhout/Huilboom clans range is larger than that indicated by the solid line, based on marked animals, and indicated approximately by the stippled line.

I - Geelhout/Huilboom clan
II - Duitsepos clan
III - Duinedam clan
IV - Elandsdrink clan

\+ - the artificial waterpoints


Elandsdrink
d
wl
W
d
w
Duinedam
Scale
5 km


IV
III
II
I
Scale
5 km

6.3.4. Habitat selection - This section is based on the distributional data collected for the Duinedam and Elandsdrink clans. The approach taken was to identify the home range and then describing the feeding areas in it, rather than each sighting location, in terms of ecological variables possibly affecting habitat choice.

As pointed out already, the two breeding groups had distinct wet and dry season home ranges. The wet season home range of both groups covered an area with a relatively high soil nutrient content (refer to Table 20), these being the Sjamarawa drainage line and the rocky periphery for the Duinedam and Elandsdrink group respectively. In Chapter 5 it was hypothesised that nutrition was responsible for this habitat selection pattern. In areas with a higher soil nutrient content, forage with a superior protein content is produced in the wet season, but this attractant disappears in the dry season, when the protein content is uniformly low. Additionally the crude protein to crude fiber ratio should be more favourable in the central, more nutrient deficient, portion of the plateau in the dry season. Also all artificial waterholes, on which the roan depend, are situated in this central part.

Observations, mainly of the Duinedam group, indicate that the animals prefer to graze in relatively open patches with good visibility and high grass biomass. Recently burned patches were preferred, having a high proportion of relatively young forage. No roan were however seen to leave their home range to graze in that of an adjoining clan which had been burned, or on any other nearby burnt patch with green grass.

The roan sought refuge in the denser patches when disturbed, always taking flight and not trying to hide like, for example, kudu.

In the dry season, when the roan were dependent on the artificial water points, they stayed within a radius of 5 km from the water.

6.4. Discussion: Roan are sedentary and form discrete clans. On the Waterberg four distinct clans were observed (Figure 33). The clan or subpopulation breaks up into unstable breeding groups, which are variable in composition. In the late dry season they splinter into smaller groups. This situation is very similar to that described for impala by Murray (1982) and roan in the Lambwe Valley in Kenya (Allsopp 1979), amongst others.

Murray (1982) found the activity centers of 82 individual female impala to be strongly clustered. Females in the same cluster (clan) had home-ranges overlapping by 73%, while overlap between females of adjacent clusters averaged 4.4%. Although female groups were unstable in composition, they were formed from a discrete set of individuals. He recognized five clans in his study area, each with 30-120 animals and ranging over 80-180 ha.

Allsopp (1979) identified two large breeding groups, numbering up to 58 individuals in the one herd, in a medium density area for roan. A group of cows, although sometimes forming subgroups, tended to stay in the same area as a bull. Little or no overlap was found between the home ranges of the two big groups. Smaller breeding groups numbering up to 20 animals were recorded but their clan association was uncertain due to lack of known animals.

The social units observed correspond to those recorded in other studies on gregarious antelope (eg. Estes 1974, Joubert 1976), namely breeding or nursery groups, bachelor groups and solitary males.

No comparable group size data is available, either because other populations were much smaller (Wilson 1975, Allsopp 1979) or the sample size was relatively small (Poché 1974). On the Waterberg the average breeding group size was 8.5 (range 2-32) during the study period. In the Lambwe Valley average group size of the two big groups was 44.6 and 35.8 animals. A bachelor group observed on 14 occasions averaged 9.5 males. In this study 76 bachelor groups had on average 3.4 members (range 2-13). Henshaw (1979) observed that roan occurred in Yankari Game Reserve, Nigeria (roan population estimated as 355), generally in groups of less than 10. In the Park W in Niger the average group size was 4.1 with a range of 1-14 (n = 37) (Poché 1974). In both studies no distinction was made between breeding and bachelor groups or solitary males.

Whereas Joubert (1976) observed a ratio of two bulls, either single or in a bachelor group, per male in a breeding group, the ratio in this study was 6.0 : 1 (241 solitary males +

260 in bachelor groups to 83 in breeding groups). Also more single males in relation to those in bachelor groups were observed in this study (1 : 1.1 versus 1 : 2.22 in the Kruger N.P.).

This difference in the ratios is expected, considering that the roan antelope on the plateau are territorial and do not form harem groups as in the Kruger N.P.. The breeding groups are not accompanied by a bull all the time, as a result of the short breeding season, and more bulls occupy territories on their own, especially during the early breeding season.

Territorial behaviour exhibited by the roan males on the plateau contrasts with the harem groups observed in the Kruger N.P., but is similar to observations made in Angola and Kenya.

Joubert (1971, 1974 and 1976) working in the Kruger National Park, found roan antelope to calve throughout the year. The same male was in attendance of a breeding group throughout the year. Roan males seemed to defend an intolerance zone around their breeding group and herding was apparently unimportant. It can be argued whether these are harem associations as in zebra, or territoriality at low population (especially male) density, particularly since behaviour patterns resemble those of the sable antelope, with males exhibiting territoriality (Grobler 1974, Joubert 1974, Owen-Smith 1977).

Oboussier (1963) working in Southern Angola, found the roan occupied a home range throughout the year in groups of 5-7 animals and that the males left the breeding groups outside the rut.

In Kenya a group of cows tended to stay in the same area as a bull. The bull was invariably in close attendance, but was never observed herding the group. Females with young calves were observed in November-December. Allsopp (1979) suggests that the roan there were truly territorial, in that they defended an area.

Owen-Smith (1977) recognises four different male mating strategies and points out that a species may make use of more than one strategy depending on local circumstances. The two strategies relevant to this discussion are i) a spatially localized dominance within a territory and ii) a mobile dominance associated with a particular female harem group. Some of the conditions that would favour territoriality, essentially a "low benefit-low cost" strategy, at Waterberg in contrast to harem groups in the Kruger N.P. are: a) Habitat seasonality - Annual grass quality cycles are more pronounced in sourveld in the

Waterberg than in sweetveld savanna, favouring a contracted breeding season. In habitat with less quality variation roan can maximise their reproductive output and produce six calves in five years but then they have to calve throughout the year. A contracted rut would increase male competion and thus favour territoriality. b) A higher local population density at Waterberg is in favour of territorial behaviour, since a harem male would be challenged more frequently as population (especially male) density increases. c) Size, cohesion, and mobility of female groups - Females in a group can come into estrous simultaneous during a contracted rut, this favours the holding of a territory. Female movement during the wet season is predictable, high quality feeding patches are selected for and early in the breeding season the limited number of artificial waterpoints are important foci on the Waterberg. In Kruger N.P. female movement is less predictable.

Sighting frequency is probably biased towards males in breeding and bachelor groups in Waterberg, because groups are more easily spotted in the relatively dense vegetation. Nevertheless the frequencies mentioned above indicate that approximately one-third to two-thirds of the adult males held a territory, which is the general rule. Territories are also typically boundary orientated with scent marking by means of dung taking place (Owen-Smith 1977).

To summarize, roan antelope are gregarious, found in breeding groups of 5-60 individuals, with a single bull in attendance at least during the rut. The breeding groups in a clan occupy fixed home ranges. This corresponds to social class C, as proposed by Jarman (1974), which also includes waterbuck, impala and greater kudu. A territory within larger home range, that overlaps with those of other males, fits Leuthold's (1977) social class 5a.

The home range as influenced by:

Method of analysis The kernel method gave a smaller home range size estimate, namely 4235 ha at the 95% level, than the size estimate of the convex polygon method with 5536 ha. By comparison, the 95% concave polygon estimate gave only 3680 ha. The harmonic mean estimate gave a totally exaggerated estimate of the home range with an unrealistic shape. The shape estimate of the convex polygon was subjectively chosen as the best suited for this study.

Group size Although in this study the larger group has the larger home range size, studies by Allsopp (1979) on roan in Kenya and by Wilson (1975) on sable in South Africa showed no relationship between group size and home range size. In the Lambe Valley, Kenya, the larger of the two groups numbered on average 45 individuals and occupied an area of approximately 1500-2000 ha. The other group averaged 36 animals and occupied 2500 ha (Allsopp 1979).

Sex and age Adult females in breeding groups and subadult bachelor males had home ranges roughly five times as large as the territory size of adult males or the home range of mostly solitary adult females. However adult males seem to range over a much larger area than adult females, during their sporadic wanderings.

Habitat A productive range allows for much more concentrated use of the home range, as shown by the Duinedam breeding group in the productive Sjamarawa drainage line. Habitat quality in terms of providing the necessary feeding areas in close proximity to suitable cover and drinking places, is probably the primary factor determining home range size.

Time of year Both the Elandsdrink and the Duinedam group ranged over larger areas during the wet season than the dry season. This is probably a result of the abundant supply of rainwater in rock pools and the assumed greater feeding selectivity, due to the greater variability in grass protein content.

Joubert (1971) also observed that the roan in the Kruger N.P. made use of distinct dry and wet season ranges, the latter being the larger.

Long term observation of home range Long term stability of the home range has been observed both in this study - one individually recognisable female stayed in same area for 9 years - and for example in the Kruger N.P. and Serengeti (Joubert 1971).

Habitat selection A suitable habitat must provide the animal with water, a balanced food supply and cover from adverse weather conditions and predators. It can be assumed that an antelope will select an area to feed in according to a different set of criteria, than an area in which to seek cover. As long as all sightings of an animal, whether feeding, resting or moving to the water, are lumped in order to determine habitat preference, the "average preference" so derived can be of little use.

The resolution at which habitat preference is determined is important. Is it at the scale of the home range (second order selection) or of habitat component within the home range (third order selection) (Johnson 1980). Recent studies show that for sedentary antelope, patch (habitat component) selection is important (Fabricius and Mentis 1992, Novellie 1990). Furthermore for a particular habitat component patch to be classified as suitable or not, actual selection by the animal must have taken place. Such spots cannot be classified correctly if they are not covered by a home range of the species. The seasonal use of areas has to be taken into consideration.

The area available to a particular species of interest must be sufficient to allow for home range selection to take place and distribution as dictated by social organization must be taken into consideration. For example, take a game reserve barely larger than the size of a normal home range, with the bachelor groups displaced by social pressure to the periphery of the breeding group's home range. The bachelor males are not displaying a habitat preference for game reserve boundaries. Despite the obvious sense of this argument, habitat preference studies for larger antelope are commonly ignore these considerations (Ben-Shahar 1988, 1990, Scogings et al. 1990).

In this study I have tried to take them into account by first determining the home range of a group, note where possible the activity of animals (feeding, walking to water or resting) when located, and then link habitat component to water, food and cover requirements.

Water was considered not to be a limiting factor, due to the good distribution of waterpoints. Henshaw (1979) observed that roan in Yankari Game Reserve occupied home ranges which in many cases were centered more than 15 km from the river. Of the major antelope species, the ones encountered farthest from water.

Cover was not considered to be critical, due to the absence of large predators, which might use cover to prey on adult roan, and of extreme weather conditions.

Nutrition was identified as the limiting factor (Chapter 5) and can be expected to determine habitat quality and choice.

Chapter 7: Management recommendations based on this study with regard to the roan population and research proposals

In this chapter management recommendations for the population of roan antelope on the Waterberg are made. They will be discussed in relation to the main topics of the study.
The management goals of the Waterberg Plateau Park are *inter alia* 1) to breed rare, indigenous herbivores to restock conservation areas/game farms, 2) to provide game viewing opportunities for tourists visiting the reserve.
Recommendations with regard to population dynamics - In 1985, 1987 and 1988, a total of 186 roan were caught. The majority, 11 groups of 10 each, were placed on Namibian game farms. These introduction were in all cases successful, in 1991 all still had roan and some have in excess of 30 now.
Some of the farmers had initial problems with the mature males killing each other.
Taking into consideration that the ecological carrying capacity of the plateau for roan is in excess of 300 and that small populations are more at risk of becoming locally extinct (Berger 1990), and also that roan are a tourist attraction, I suggest that the minimum population in the reserve should be 200 and the maximum about 300. Roan should be caught about every third to fourth year to keep the population within these limits. It is felt that this will be a reasonable compromise between capture stress and social disruption on the one hand, and making the capture operation viable on the other. A preliminary capture program is presented in Table 37. The present method of capture, darting the roan individually from a helicopter, puts considerable stress on the population. After a capture operation the remaining animals are very wary for at least half a year. This makes game viewing in the wooded savanna very frustrating, since flight distance is usually more than the distance at which the animal is observable.
Roan antelope have a complex social system, which is disturbed with each capture. The higher the percentage of animals caught, the more this social system is disturbed. This aspect is probably partly responsible for the population growth lag after the 1987 and 1988 captures.

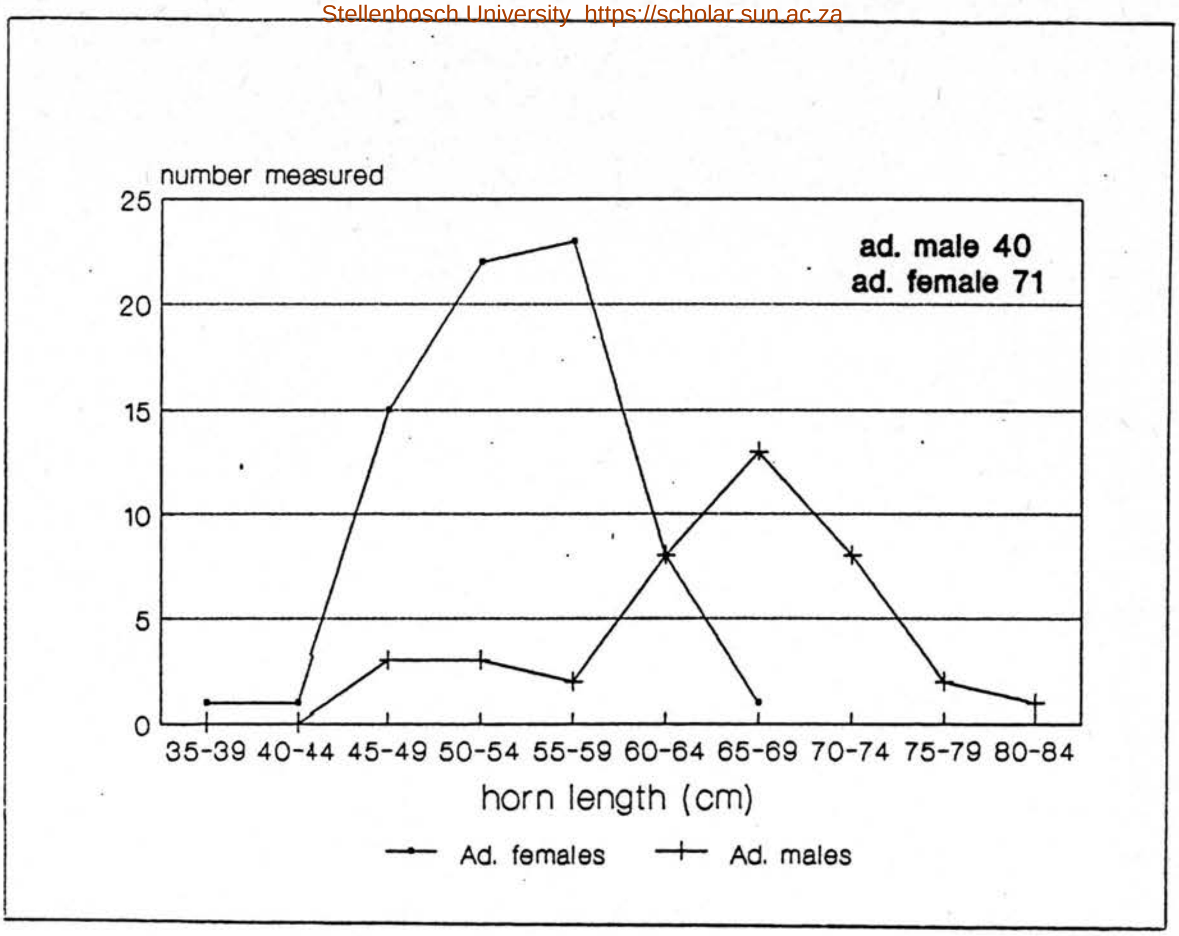


Figure 34: Recorded horn length measurements of adult animals during captures and on dead animals (sample size 40 adult males and 71 adult females).

Table 36

Roan antelope captured and projected captures

	males				females				
year	ad.	sub.1	sub.2	juv.	ad.	sub.1	sub.2	juv.	total
1984									
1985	12	6	5	0	26	15	4	4	72
1986									
1987	8	6			21	2			37
1988	21	8		0	38	9		1	77
1989									
1990									
1991									
1992									
1993	10	5	5		15	10	5		50
1994									
1995									
1996	15	8	5		17	15	10		70
1997									
1998									
1999	15	8	5		17	15	10		70
2000									
caught	41	20	5	0	85	26	4	5	186
projected	40	21	15	0	49	40	25	0	190
total	81	41	20	0	134	66	29	5	376

In managing the population as closely as possible to what seems natural, it is suggested that the adult sex ratio be kept close to 1:2.

Every year a few old males, some of them already blind in one eye as a result of fighting injuries, could be made available as trophy animals. The trophy quality of the males is certainly good, there is a strong demand for roan trophies and good prices are paid. Horn length measurements of 40 adult males and 71 adult females, are shown in Figure 34. These are measurements taken during the capture operations and from natural mortalities found. The Rowland Ward minimum horn length is 74.9 cm. It is felt that this aspect should get attention. Roan trophy fees are considerable and every year two to five old males could be hunted. The revenue thus obtained could pay for the proper monitoring of all rare species on the Waterberg, which would in turn allow for better management.

Recommendations with regard to feeding habits - The quality of the grazing available to the roan, seems to be the most limiting environmental factor on the Waterberg. The grazing is known to be poor, chemical analyses indicate a low nutritive quality, and roan appear to respond well to supplementary licks.

Grass quantity itself is adequate, even that of the preferred species. It is essential that the burning regime on the plateau be maintained, in order to keep the grass sward vigorous. Monitoring of the grass sward is essential. Emphasis needs to be placed on species composition and on nutritive quality of the preferred species.

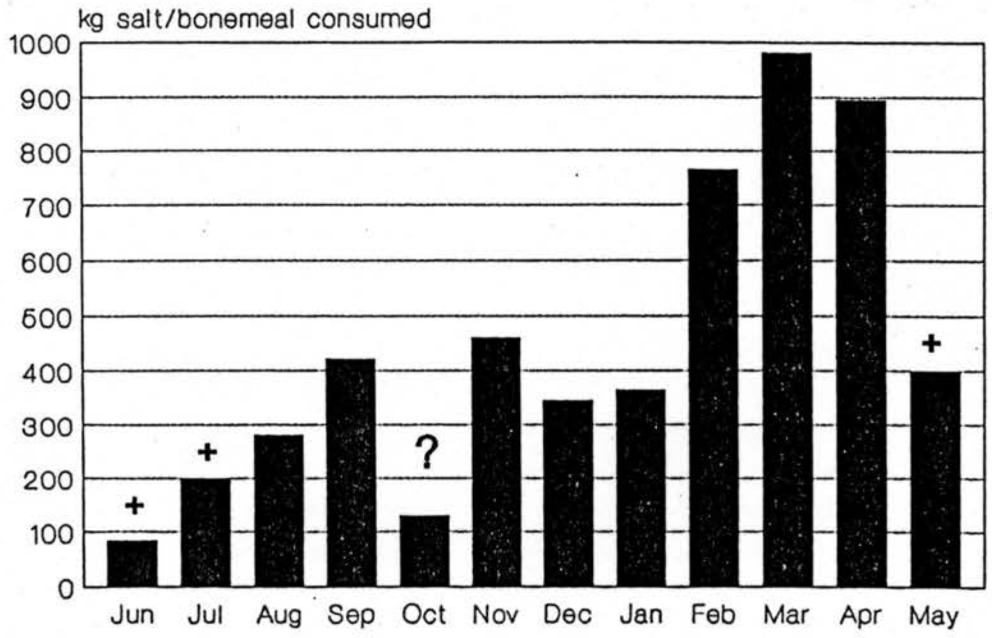
Feeding of a mineral lick must be maintained and the consumption should be monitored on a monthly basis (Figure 35).

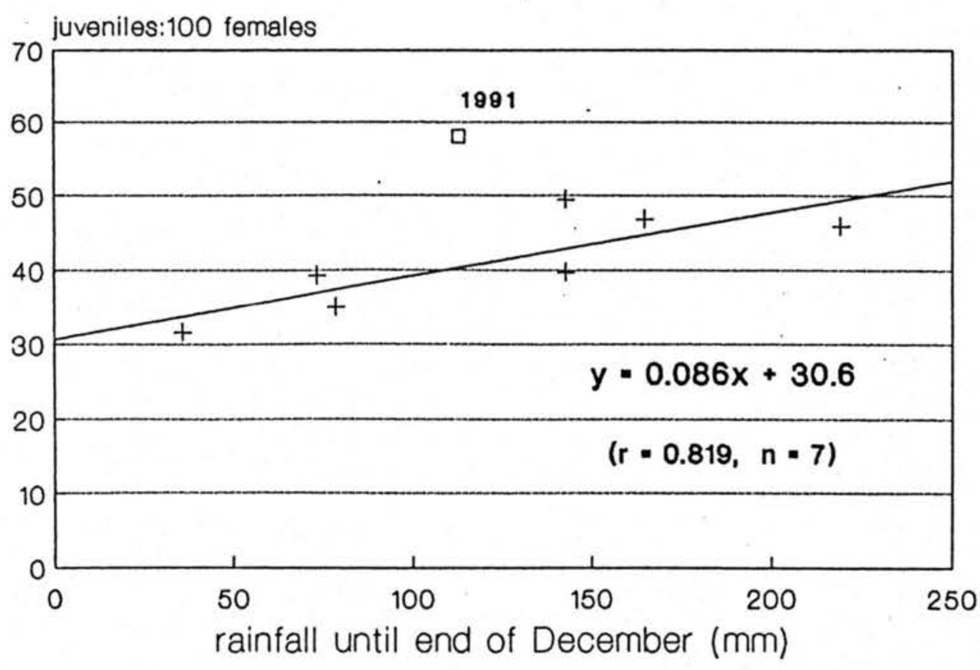
The female infant ratio should be determined at the August waterhole count in order to detect changes such as those which occurred in 1991, after lick feeding had been initiated (Figure 36).

Direct feeding competition should only occur between the roan, sable, tsessebe and red hartebeest, all of which are adapted to feeding selectively in a sward of medium height.

Figure 35: Monthly bonemeal/salt consumption during 1990/91 by all game on the plateau.

Figure 36: The expected and recorded juvenile: female ratio during 1991 (juv.: 100 adult females), after having been fed bonemeal/salt for one year. The + marks and the regression line indicate that observed in the years when no lick was fed.


kg salt/bonemeal consumed
1000
900
800
700
600
500
400
300
200
100
0
+
+
?
+
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Jan
Feb
Mar
Apr
May


juveniles:100 females
70
60
50
40
30
20
10
0
1991
y = 0.086x + 30.6
(r = 0.819, n = 7)
0
50
100
150
200
250
rainfall until end of December (mm)

<u>Recommendations with regard to sociology and use of space</u> - It is recommended that the clans be considered separately, when deciding on removal figures. Based on the roan antelope's social organization, it felt that distinct clans on the plateau should be maintained to maintain productivity. It is thought that established breeding groups will breed more prolifically than newly formed groups in vacated areas. The Duinedam clan, well studied and with many marked individuals, should be kept as control group. No individuals should be captured out of this clan and new animals should be eartagged to facilitate accurate monitoring.

<u>Monitoring requirements</u> - Adaptive management, which is applied by the Ministry of Wildlife, Conservation and Tourism, is only possible when management action is monitored, evaluated and adapted. This process requires that environmental parameters, such as grazing or cover, which have to be monitored, are identified. These parameters can then be evaluated against guidelines once critical limits for these factors are determined.

This research project has identified some of the monitoring requirements for management of the roan population on the plateau and also served as a baseline survey. Guidelines for critical limits, as determined by ecological processes or management goals, have also been identified.

The population model, although in need of evaluation and refinement, indicates how the population dynamics parameters which were monitored, can be expected to behave. Deviations should be carefully examined and analysed to increase our understanding of roan population dynamics.

Parameters which should be monitored annually are total population size and age and sex ratios. The Waterberg, because of its size and management objectives, requires active management. The roan population is very much part of this process. An accurate assessment of population size is thus essential and can be most effectively obtained during the annual waterhole counts. The age/sex ratios enable one to anticipate population changes.

It is essential to monitor whether the roan have access to an adequate nutrient supply. How best to do so still needs further research, but at this stage it is recommended that faecal samples of adults be collected, separately for the sexes, in the dry season (August/September) and analyzed for crude protein, neutral detergent fiber, phosphate and calcium. This chemical analysis probably also has an

indicator value for species with similar feeding requirements ie. sable, tsessebe and red hartebeest.
Serum samples should be collected where possible and tested for anti-bodies, especially for anthrax, and blood parasites.
Post-mortems should be conducted where possible, when carcasses are found and the skulls from all carcasses should be collected and aged. However with a conservative average annual mortality rate of 15% for all age/sex classes, the few carcasses recovered each year, are not representative of the population. This is especially the case for the small carcasses of juveniles, which are much more difficult to find in the field and disintegrate faster, than those of adults.

Research needs - Four environmental factors that affect the roan antelope on the plateau can be changed by management. They are grazing, water, cover and predation.
Of these, grazing seems to be the most important factor as far as marginal response through improved management action is concerned. The other factor that could influence the roan population is predation by leopard, should alternative prey become scarce. Water and cover availibilty do not seem to be limiting the roan.
The limiting factor with regard to grazing is its quality. This needs to be better quantified than was possible in the present study. It is also necessary to determine whether nutritive quality could be enhanced through management, e.g. by changing the burning regime or introducing elephant, both of which would enhance nutrient cycling, and how limiting nutrients could be supplement most efficiently.
An interesting study would be to determine habitat use and territorial behaviour in more detail when global position system (GPS) technology becomes available in "radio collar" form for antelope. With the present radio collar technology it is not feasible to undertake such a study because of the disturbance involved and the cost of tracking several animals simultaneously and continuously over a fairly large area.

Summary

This study was undertaken in the Waterberg Plateau Park in northern Namibia. Field work took place between January 1988 and September 1989; however relevant information collected since, has been included.
The roan antelope population in the reserve stems from re-introduced animals. A total of 93 were brought in between 1975 and 1981. By 1984 the population peaked at 275 individuals. 109 roan were captured and sold before the start of the study. A further 77 animals (one-third of the population) were removed during the study.
The main objective of the study was to develop a better understanding of the management requirements for this population of rare antelope.
Approximately one-fifth (32 individuals) of the population was marked with eartags and or plastic collars. Five individuals were radio-collared. It is the first time that a detailed study was undertaken on roan antelope in such a large study area (40 000 ha), with such a large study animal population (200+ roan) and so many marked individuals (32).
Chapter 3 deals with population dynamics. It is believed that the entire population was accurately counted, aged and sexed. Counts were primarily undertaken at waterholes in the late dry season. The waterhole counts are compared with helicopter censuses. The percentage of roan counted during a particular helicopter count was dependent on the time of year - in the late dry season visibility was the best.
In 1984, prior to any removals, the adult sex ratio was 1:3. In 1988, after 126 adults had been removed in a 1:2 sex ratio, the adult sex ratio had dropped to 1:1.2. The adult sex ratio was in favour of females, despite the absence of large predators able to kill adults.
The majority of calves were born during the wet season, from the end of August to March. In the Kruger National Park (KNP) calves are dropped throughout the year. A positive relationship between early season rainfall and the calf crop in the subsequent year was found.
The ratio of juveniles per 100 adult females averaged 41.1 over seven years, during the August waterhole counts, juveniles are then approximately 8 months old. The range of this ratio was narrower than in the KNP and can be improved. Recorded mortality was to small to identify significant factors. It is interesting that, of the 21 carcasses found, 4 juveniles/ subadults were preyed on by leopard. No adult female carcasses were found, in comparison to 10 adult male

carcasses. The cause of death could not be determined for half of these, while the other half died of old age (molar I worn right down).

Two deterministic population models were developed for exploratory simulations and are presented in Chapter 4. The first model attempts to depict population change from 1975 to 1991, when on the whole the input data was less reliable. The second model makes use of the more accurate data for the period 1984 to 1991. Both simulations were fairly successful, judging by good correlation coefficients obtained with the actual counts.

A lot of emphasis has been placed on possible nutrient deficiencies, since it is known that the Kalahari sands on the plateau are very nutrient poor. This aspect and nutrition in general is covered in chapter 5. Grass nutrient concentrations were spatially very variable in the wet season and the roan selected for areas where the crude protein content of the grass was high. These where on the plateau periphery and the Sjamarawa drainage line where soil nutrient levels were higher than elsewhere. In the dry season, nutrient content of the grass was much more uniform between the different habitats. Crude fiber concentrations were probably more favourable on the central portion of the plateau, then selected by roan. Grass phosphate concentrations are significantly lower in the Kalahari sand than in sweet veld. Calcium values are comparatively low, but can still be regarded as normal. The Ca:P ratio is particularly unfavourable in the late dry season.

Simple nutrient budgets revealed that protein and phosphate requirements were probably not met in the dry season. Based on hand selected forage samples and cattle requirements, calculation shows that adult roan obtained 15-28% of their crude protein requirements and approximately 10% of the phosphate in the dry season.

The social system of the roan is described in Chapter 6. Four different clans were recognized, each with a distinct home range. The breeding groups in each clan were unstable, splitting up and rejoining at random. There were significantly more large groups in the population in 1984, prior to the captures, than after the captures in 1988 and during the study period.

Adult males exhibited territoriality during the breeding season. This is in contrast to most other studies where harem groups had been observed. Significantly more males were observed on their own or in breeding groups, as dominant males, in the two quarters from July to December compared to the first two quarters. Outside the breeding season, dominant males rejoined bachelor groups or remained solitary. Territoriality is discussed comparing the environmental factors between Waterberg and KNP.

Home range size and configuration were described using different methods, of which the convex polygon proved the most suitable approach for this study and its objectives. Using this method, home range size averaged 4800 ha for two clans and the territory size of one male was estimated to be 1200 ha in a much bigger home range. Distinct wet - and dry season ranges could be distinguished, the former being larger.

Habitat selection is discussed, and was determined primarily through feeding requirements. Forage quality was identified as the major limiting factor and thus determined primarily habitat use.

In Chapter 7 management recommendations and research proposals are made to ensure sustainable utilisation, both with regard to live capture and tourist game viewing.

The roan population should fluctuate between 200 and 300 animals, which is below environmental carrying capacity. Captures should take place every three to four years, being a compromise between capture stress and social disruption and economical viability.

Licks were provided towards the end of the study and seem to be beneficial, in that a better calf crop is obtained. Horn measurements indicate that good trophies can be found on the plateau and trophy hunting should be considered as a form of utilisation. Clans should be considered separately, when deciding on removing animals. The Duinedam clan should be used as a control and individuals in this group should be marked at intervals to facilitate monitoring in future.

Population parameters need to be monitored on an annual basis. Forage quality should be monitored through dung analysis and was identified as a research priority. Forage quality needs to be assessed on a wider scale than was possible in this study. Can forage quality be improved through management and how to best supplement the animals.

References:

Allen-Rowlandson,T.S. 1980. The social and spatial organization of the greater kudu (Tragelaphus strepsiceros) Pallas 1766, in the Andries Vosloo Kudu Reserve, Eastern Cape. M.Sc.thesis Rhodes University.

Allsop,R. 1979. Roan antelope population in the Lambe valley, Kenya. J.Appl.Ecol. 16:109-115

Anderson,D.J. 1982. The home-range: a new nonparametric estimation technique. Ecology 63:103-112

Ansell,W.F.H. 1960. The breeding of some larger mammals in Northern Rhodesia. Proc.zool.Soc.Lond. 134:251-274

Ansell,W.F.H. 1972. Part 2. 15 Family Artiodactyla, pp 1-84 in The mammals of Africa: an identification manual. Eds J.Meester & Setzer,H.W. Washington D.C.: Smithsonian Institution Press.

Backhaus,D. 1959. Beobachtungen über das Freileben von Lelwel-Kuhantilopen (Alcelaphus buselaphus lelwel) und Gelegenheitbeobachtungen an Sennar-Pferdeantilopen (Hippotragus equinus bakeri). Z. Säugetierk. 24(1-2):1-34

Beasom,S.L.& Burd,J.D. 1983. Retention and visibility of plastic ear tags on deer. J.Wildl.Manage. 47(4):1201-1203

Bell,R.H.V. 1981. An outline of a management plan for Kasungu National Park, Malawi. in Jewell,P.A.& Holt,S. (eds.) Problems in management of locally abundant wild mammals. Academic Press: New York

Belonje,P.C.& van den Berg,A. 1980a. The use of faecal analyses to estimate the phosphorus intake by grazing sheep. 1. The use of pool instead of individual samples. Onderstepoort J.Vet.Res. 47:163-167

Belonje,P.C.& van den Berg,A. 1980b. The use of faecal analyses to estimate the phosphorus intake by grazing sheep. 2. The repeatability of the technique and the influence of varying the phosphorus intake. Onderstepoort J.Vet.Res. 47:169-172

Ben-Shahar,R. 1986. The conservation of endangered ungulates in the Waterberg,Transvaal. M.Sc.thesis, University of Pretoria, Pretoria.

Ben-Shahar,R.& Skinner,J.D. 1988. Habitat preferences of African ungulates derived by uni- and multivariate analysis. Ecology 69:1445-1451

Ben-Shahar,R. 1990. Resource availability and habitat preferences of three African ungulates. Biol.Cons. 54:357-365

Berger,J. 1990. Persistence of different-sized populations: an empirical assessment of rapid extinctions in bighorn sheep. Conservation Biology 4(1):91-98

Berry,H.H. & Louw,G.N.1982a. Nutritional measurements in a population of free-ranging wildebeest in the Etosha National Park. Madoqua 13(2):101-125

Berry,H.H. & Louw,G.N.1982b. Seasonal nutritive status of wildebeest in the Etosha National Park. Madoqua 13(2): 127-139

Berry,H.H. 1981. Population structure, mortality patterns and a predictive model for estimating future trends in wildebeest numbers in the Etosha National Park. Madoqua 12(4):255-266

Best,E.B., Palmer,A.W., Shepard,T. & Wilson,V.J. 1970. Some notes on the present day status of roan Hippotragus equinus, in Rhodesia. Arnoldia 5(2):1-10

Bigalke,R.C.H. 1958. On the present status of ungulate mammals in South West Africa. Mammalia 22:478-497

Bransby,D.I. 1981. The value of veld and pasture as animal feed. pp.173-214 in Tainton,N.M. (ed.) Veld and pasture management in South Africa. Shuter & Shooter: Pietermaritzburg

Brooks,P.M. 1982. Zebra, wildebeest and buffalo sub-population areas in the Hluhluwe-Corridor-Umfolozi Complex, Zululand, and their application in management. S.Afr.J.Wildl.Res. 12:140-146

Button,P. 1986. The estimation of home range. Unplublished Honours project University of Cape Town, Cape Town

Child,G. & Wilson,V.J. 1964. Observations on ecology and behaviour of roan and sable in three tsetse control areas. Arnoldia Rhod. 1(16):1-8

Church,D.C. 1979. Digestive physiology and nutrition of ruminants. Corvallis: O&B Books

Clark,T.P.& Gilbert,F.F. 1982. Ecotones as a measure of deer habitat quality in central Ontario. J.Appl.Ecol. 19:751-758

Don,B.A.C.and Rennolls 1983. A home range model incorporating biological attraction points. J.Anim.Ecol. 52:69-81

Dott,H.M. 1987. Reproduction as a factor in adaption. S.Afr. J.Sci. 83:620-623

Drevemo,S., Grootenhuis,J.G. & Karstad,L. 1974. Blood parameters in wild ruminants in Kenya. J.Wildl.Dis. 10:327-333

Dunn,J.E.& Gipson,P.S. 1977. Analysis of radio telemetry data in studies of home range. Biometrics 33:85-101

du Plessis,S.S. 1972. Ecology of blesbok with special reference to productivity. Wildlife Monographs No. 30

Engels,E.N.A. 1981. Mineral status and profiles (blood, bone and milk) of the grazing ruminant with special reference to calcium, phosphorus and magnesium. S.Afr.J.Anim.Sci. 11:171-182

Erasmus,T., Penzhorn,B.L.and Fairall,N. 1978. Chemical composition of faeces as an index of veld quality. S.Afr.J.Wildl.Res.8:19-24

Estes,R.D. 1974. Social organization of African bovids. Proc. Symp.: The behaviuor of ungulates and its relation to management. Univ.Calgary, Alberta, Canada 2-5.November 1971 IUCN Publications n.s. 24:166-205

Estes,R.D.& Estes,R.K. 1976. Behaviour and ecology of the giant sable. In: National Geographic Society Research Reports, 1968 projects. pp 115-129 Washington D.C.

Fabricius,C.& Mentis,M.T. 1992. Modelling the habitat relations of kudu in arid savanna. S.Afr.J.Sci. 88:280-284

Fairall,N. 1968. The reproductive seasons of some mammals in the Kruger National Park. Zool.Afr. 3:189-210

Fourie,J.H., Engels,E.A.N.& De Bruyn,Heila L.H.C. 1986. The influence of stocking rate and grazing system on the crude protein content and digestibilty of Tarchonanthus veld in the Northern Cape. J.Grassl.Soc. South.Afr. 3(2):62-69

Franzmann,A.W. 1972. Environmental sources of variation of bighorn sheep physiologic values. J.Wildl.Mgmt. 36:924-932

Franzmann,A.W.& LeResche,R.E. 1978. Alaskan moose blood studies with emphasis on condition evaluation. J.Wildl.Manage. 42(2):334-351

Fuggle,R.F.& Rabie,M.A. (eds) 1983. Environmental concerns in South Africa. Juta & Co: Cape Town

Gaerdes,J. 1967. Änderungen im Wildbestand von Südwestafrika seit 1910 - Pferde-Antilopen in SWA. supplement to Mitteilungen der S.W.A. Wissenschaftliche Gesellschaft 7(11):1-6

Gates,C.C.& Hudson,R.J. 1981. Weight dynamics of wapiti in the boreal forest. Acta Theriol. 27:407-418

Geerling,C. 1979. The use of faecal analysis in studying food habits of West African ungulates. in: Ajayi,S.S. & Halstead,L.B. (eds) Wildlife management in savanna woodland. London: Taylor & Francis

Geerling,C.& Bokdam,J. 1973. Fauna of the Comoe National Park, Ivory Coast. Biol.Cons. 5.251-257

Grant,C.C. 1989. Development of a system classifying and monitoring the availability of minerals to cattle in the ranching areas of SWA/Namibia. D.VSc. thesis University of Pretoria, Pretoria

Grobler,J.H. 1974. Aspects of the biology, population ecology and behaviour of the sable Hippotragus niger niger (Harris, 1838) in the Rhodes Matopos National Park, Rhodesia. Arnoldia Rhod. 7(6):1-36

Grobler,J.H. 1981. Feeding behaviour of sable Hippotragus niger niger (Harris, 1838) in the Rhodes Matopos National Park, Zimbabwe. S.Afr.J.Zool. 16:50-58

Hegenberger,W. 1990. The geology of the Waterberg. Unpubl. manuscript 7 pp. 9 illust.

Heitkönig,I.M.A. 1987. The conservation of roan, sable and tsessebe in the Waterberg. African Wildlife 41(4):

Henshaw,J. 1979. Notes on habitat relationships of ungulates in Yankari Game Reserve, Nigeria. Mammal Rev. 9(1):47-52

Hofmeyr,J.M. 1973. The adaption of wild animals translocated to new areas in South West Africa. Proc.3rd Wld.Congr. Anim.Prod. Melbourne pp.126-131

Hofmeyr,J.M. 1974. Development in the capture and airlift of roan antelope (Hippotragus equinus equinus Desmarest) under narcosis to the Etosha National Park. Madoqua 1(8):37-48

Holeckeck,J.L., Vavra,M. & Pieper,R.D. 1982. Methods for determining the nutritive quality of range ruminant diets: a review. J.Anim.Sci. 54:363-376

Howard,P.C. 1986. Spatial organization of common reedbuck with special reference to the role of juvenile dispersal in population regulation. Afr.J.Ecol. 24:155-171

Huntley,B.J. 1982. Southern African savannas. p101-119 in: Huntley,B.J.& Walker,B.H. (eds.) Ecology of tropical savannas. Berlin: Springer Verlag

Jankowitz,W.J. 1983. Die plantekologie van die Waterberg Platopark. D.Sc.thesis University of the Oranje Freestate

Jankowitz,W.J.& van Rensburg,W.L.J. 1985. Die basale bedekking en die weibare opbrengs van die sleutelgrasse en die dravermoë van die kruidstratumvan die plantgemeenskappe in die Waterberg-platopark. Madoqua 14(3):305-313

Jankowitz,W.J.& Venter,H.J.T. 1987. Die plantgemeenskappe van die Waterberg-platopark. Madoqua 15(2):97-146

Jarman,P.J. 1974. The social organization of antelope in relation to their ecology. Behaviour 48:216-267

Jenrich,R.I. and Turner,F.B. 1969. Measurement of non-circular home range. J. Theor.Biol. 22:227-237

Jewell,P.A. 1966. The concept of home range in mammals. Symp.zool.Soc.Lond. 18:85-109

Johnson,D.H. 1980. The comparison of useage and availability measurements for evaluating resource preference. Ecology 61:65-71

Joubert,E.& Eloff,F.C. 1971. Notes on the ecology and behaviour of the black rhinoceros <u>Diceros bicornis</u> Linn. 1758 in South West Africa. Madoqua 1(3):5-53

Joubert,E.& Mostert,P.K.N. 1975. Distribution patterns and status of some mammals in South West Africa. Madoqua 9:5-44

Joubert,S.C.J. 1971. A study of the social behaviour of the roan antelope, <u>Hippotragus equinus equinus</u>, in the Kruger National Park. M.Sc. thesis University of Pretoria

Joubert,S.C.J. 1974a. The management of rare ungulates in the Kruger National Park. J.sth.Afr.Wildl.Mgmt Ass.4(1):67-69

Joubert,S.C.J. 1974b. The social organization of the roan antelope, <u>Hippotragus equinus</u>, and its influence on spatial distribution of herds in the Kruger National Park. Proc. Symp.: The behaviour of ungulates and its relation to management. Univ.Calgary, Alberta, Canada 2-5.November 1971 IUCN publication pp.661-675

Joubert,S.C.J. 1976. The population ecology of the roan antelope, <u>Hippotragus equinus equinus</u> (Desmarest, 1804), in the Kruger National Park. D.Sc.thesis, University of Pretoria

Kingdon,J. 1982. East African Mammals. Vol 3 Part D Academic Press: London

Kruger,A.S. 1988. 'n Evaluering van <u>Stipagrostis uniplumis</u>. Agri Info 1(2):2-3 Directorate Agriculture and Forestry, Namibia

Leslie,D.M. and Starkey,E.E. 1985. Fecal indices to dietary quality of cervids in old-growth forests. J.Wildl. Manage. 49:142-146

Leslie,D.M. and Starkey,E.E. 1987. Fecal indices to dietary quality: a reply. J.Wildl.Manage. 51(2):321-325

Leuthold,W. 1977. African ungulates. A comparative review of their ethology and behavioural ecology. Zoophysiology & Ecology 8. New York: Springer Verlag

Mason,D.R. 1990. Juvenile survival and population structure of blue wildebeest and warthogs in the Central Region of the Kruger National Park during the mid-summer drought of 1988/89. Koedoe 33(1):29-45

McDowell,L., Conrad,J.H.& Ellis,G.L. 1984. Mineral deficiencies and imbablances and their diagnosis. pp.67-88 in: Gilchrist,F.M.C.& Mackie,R.I. (eds.) Herbivore nutrition in the subtropics and tropics. The Science Press: Craighall

McLeod,M.N. 1974. Plant tannins - their role in forage quality. Nutr.Abstr.and Rev. 44:803-815

Melton,D.A. & Melton,C.L. 1982. Condition and mortality of waterbuck (Kobus ellipsiprymnus) in the Umfolozi Game Reserve. Afr.J.Ecol. 20:89-103

Melton,D.M. 1987. Habitat selection and resource scarcity. S.Afr.J.Sci. 83:646-650

Metzgar,L.H. 1972. The measurement of home-range shape. J.Wildl.Mgmt 36:643-645

Milligan,K., Ajayi,S.S.& Hall,B. 1982. Density and biomass of large herbivore community in Kainji Lake National Park, Nigeria. Afr.J.Ecol. 20:1-12

Moen,A,N. 1973. Wildlife ecology - an analytical approach. Freeman & Co: San Francisco

Monro,R.H.& Skinner,J.D. 1979. A note on the condition indices for adult male impala, Aepyceros melampus. S.Afr.J.Anim.Sci. 9:47-51

Moss,C. 1988. Elephant memories - thirteen years in the life of an elephant family. Fontana/Collins: England 336 pp.

Mossolow,N. undated. Waterberg - Beitrag zur Geschichte der Missionsstation Otjozondjupa, des Kambazembi-Stammes und des Hererolandes. 56 pp. Printed by John Meinert, Windhoek

Mould,E.D. and Robbins,C.T. 1981. Nitrogen metabolism in elk. J.Wildl.Manage. 45:323-334

Mukinya,J.G. 1973. Density, distribution, population structure and social organization of the black rhinoceros in Masai Mara Game Reserve. E.Afr.Wildl.J. 2:385-400

Murray,M.G. 1982. Home range, dispersal and the clan system of impala. Afr.J.Ecol. 20:253-269

Novellie,P. 1986. Relationships between rainfall, population density and the size of the bontebok lamb crop in the Bontebok National Park. S.Afr.J.Wildl.Res. 16:39-46

Novellie,P. 1990. Habitat use by indigenous grazing ungulates in relation to sward structure and veld condition. J.Grassl.Soc.South.Afr. 7(1):16-23

O'Reagain,P.J.& Mentis,M.T. 1988. Seasonal changes in the quality of the diet selected by cattle grazing the Natal sour sandveld. J.Grassl.Soc.South.Afr. 5(1):48-51

Oboussier,H. 1963. Die Pferdeantilope (Hippotragus equinus cottoni, Dollman and Burlace 1928) Ergebnisse der Forschungsreisen nach Südangola. Z.Morph.Okol.Tiere 52:688-713

Owen-Smith,N. 1977. On territoriality in ungulates, and an evolutionary model. Q.Rev.Biol. 52:1-38

Owen-Smith,N. 1982. Factors influencing the consumption of plant products by large herbivores. pp.359-404 in: Huntley,B.J. & Walker,B.H. (eds.) The ecology of tropical savannas. Ecological Studies 42 Berlin: Springer Verlag

Owen-Smith,N. 1984. Demography of greater kudu _Tragelaphus strepsiceros_ in relation to rainfall. Acta Zool. Fennica 172:197-199

Owen-Smith,N. 1985. Niche separation among African ungulates. pp 167-171 in: Vrba,E.S.(ed.) Species and speciation. Transvaal Museum Monograph No.4 Transvaal Museum, Pretoria.

Owen-Smith,R.N. 1988. Megaherbivores - the influence of very large body size on ecology. Cambridge University Press: Cambridge

Owen-Smith,N. 1990. Demography of a large herbivore, the greater kudu _Tragelaphus strepsiceros_, in relation to rainfall. J.Anim.Ecol. 59:893-913

Owen-Smith,N.& Cooper,S.M. 1987. Palatability of woody plants to browsing ruminants in a South African savanna. Ecology 68(2):319-331

Owen-Smith,N.& Cooper,S.M. 1989. Nutritional ecology of a browsing ruminant, the kudu (Tragelaphus strepsiceros), through the seasonal cycle. J.Zool.,Lond. 219:29-43

Owen-Smith,N.& Novellie,P. 1982: What should a clever ungulate eat? Am.Nat. 119:151-178

Pienaar,U.de V. 1974. Habitat-preference in South African antelope species and its significance in natural and artificial distribution patterns. Koedoe 17:185-195

Poché,R.M. 1974. Notes on roan antelope in West Africa. J.Afr.Ecol. 11:963-968

Putman,R.J.and Hemmings,G.J. 1986. Can dietary quality of free-ranging ungulates be simply determined from faecal chemistry? Acta Theriol. 31(20):257-270

Read,M.V.P., Engels,E.A.N.& Smith,W.A. 1986. Phosphorus and the grazing ruminant. 2.The effects of supplementary P on cattle at Glen and Armoedsvlakte. S.Afr.J.Anim.Sci. 16:7-12

Renecker,L.A.and Hudson,R.J. 1985. Estimation of dry matter intake of free-ranging moose. J.Wildl.Manage. 49:785-792

Rexstad,E.A., Miller,D.D., Flather,C.H., Anderson,E.M., Hupp.J.W. & Anderson,D.M. 1988: Questionable multi-variate statistical inference in wildlife habitat and community studies. J.Wildl.Mange. 52(4):794-798

Rutherford,M.C. 1975. Aspects of ecosystem functioning in a woodland savanna in South West Africa. D.Sc. thesis University of Stellenbosch: Stellenbosch

Samuel,M.D.& Garton,E.O. 1987. Incorporating activity time in harmonic home range analysis. J.Wildl.Mgmt. 51(1):254-257

Scogings,P.F., Theron,G.K.& Bothma,J.du P. 1990. Two quantitative methods of analysing ungulate habitat data. S.Afr.J.Wildl.Res. 20(1):9-13

Scrivner,J.H., Vaughn,C.E.& Jones,M.B. 1988. Mineral concentration of black-tailed deer diets in California chaparral. J.Wildl.Manage. 52(1):37-41

Seal,U.S., Ozoga,J.J., Erikson,A.W. & Verme,L.J. 1972. Effects of immobilization of blood analyses of white-tailed deer.J.Wildl.Mgmt. 36:1034-1040

Sekulic,R. 1976. A case of adoption in the roan antelope in Kenya. Säug.Mitt. 24:235-238

Sekulic,R. 1978a. Note on interactions between sable (Hippotragus niger) and roan (Hippotragus equinus) antelopes in Kenya. J.Mammal. 59(2):444-446

Sekulic,R. 1978b. Roan translocation in Kenya. Oryx 14(3): 213-217

Shortridge,G.C. 1934. The mammals of South West Africa. Vol. II Heineman: London

Sinclair,A.R.E. 1974a. The natural regulation of buffalo populations in East Africa. III.Population trends and mortality. E.Afr.Wildl.J. 12:185-200

Sinclair,A.R.E. 1974b. The natural regulation of buffalo populations in East Africa. IV.The food as a regulating factor, and competition. E.Afr.Wildl.J. 12:291-311

Skinner,J.D.& Smithers,R.H.N. 1990. The Mammals of the Southern African Subregion. University of Pretoria: Pretoria

Skinner,J.D.& van Jaarsveld,A.S. 1987. Adaptive significance of restricted breeding in Southern African ruminants. S.Afr.J.Sci. 83:657-663

Smithers,R.H.N. 1966. The mammals of Rhodesia, Zambia and Malawi. London: Collins

Smuts,G.L. 1974. Game movements in the Kruger National Parkand their relationship to the segregation of sub-populations and the allocation of culling compartments. J.sth.Afr.Wildl.Mgmt.Ass. 4(1):51-58

Stanley-Price,M.R. 1978. The nutritional ecology of Coke's hartebeest in Kenya. J.Appl.Ecol. 15:33-49

Stanley-Price,M.R. 1977. The estimation of food intake and its seasonal variation in the hartebeest. E.Afr.Wildl.J. 15:107-124

Starfield,A.M.& Bleloch,A.L. 1986. Building models for conservation and wildlife management. Macmillan Publishing Co.: New York

Starfield,A.M., Joubert,S.C.J., Cohen,B.J., Hague,E.K.& Stein,D.J. 1979. An exploratory model of impala population dynamics. in: Getz,W.M.(ed.) Lecture notes in Biomathematics 33:338-355 Springer Verlag

Starfield,A.M., Smuts,G.L.& Shiell,J.D. 1976. A simple wildebeest population model and its application. S.Afr.J.Wildl.Res. 6(2):95-98

Stark,M.A. 1986a. Plant communities use and spatial overlap of the more common large herbivores, Benoue National Park, Cameroon. Mammalia 50(2):185-192

Stark,M.A. 1986b. The numbers, seasonal distribution pattern, densities and biomass of the large herbivores, Benoue National Park, Cameroon. Mammalia 50(3):341-350

'tMannetje,L. 1984. Nutritive value of tropical and sub-tropical pastures, with special reference to protein and energy deficency in relation to animal production. pp.51-66 in: Gilchrist,F.M.& Mackie,R.I. (eds.) Herbivore nutrition in the subtropics and tropics. Craighall: The Science Press

Van der Merwe,J.H. (ed) 1983. National atlas of South West Africa (Namibia). University of Stellenbosch: Stellenbosch

Van der Walt,P.T. 1989. Suidwes-Afrika: Natuurbewaring in perspektief. Agri-info 2(1):4-7

Van Lavieren,L.P.& Esser,J.D. 1979. Numbers, distribution and habitat preference of large mammals in Bouba Ndjida National Park, Cameroon. Afr.J.Ecol. 17:141-153

Van Winkle,W. 1975. Comparison of several probabilistic home-range models. J.Wildl.Mgmt. 39:118-123

Van Winkle,W.,Martin,D.C.and Sebetich,M.J. 1973. A home range model for animals inhabiting an ecotone. Ecology 54:205-209

Venter,J.& Hopkins,M.E. 1988. Use of a simulation model in the management of a lion population. S.Afr.J.Wildl.Res. 18(4):126-130

Voigt,D.R.& Tinline,R.R. 1980. Strategies for analyzing radio tracking data. pages 387-404 in: Amlaner,C.J.& MacDonald,D.W. (eds.) A handbook on biotelemetry and radio tracking. Pergamon Press,Oxford, United Kingdom

Walter,H.& Volk,O.H. 1954. Grundlagen der Weidewirtschaft in Südwestafrika. 281 pp Ulmer: Stuttgart

White,T.C.R. 1978. The importance of a relative shortage of food in animal ecology. Oecologia (Berlin) 33:71-86

Wilson,D.E. 1975. Factors affecting roan and sable antelope populations on nature reserves in the Transvaal with particular reference to ecophysiological aspects. D.Sc. thesis University of Pretoria

Wilson,D.E., Bartsch,R.C., Bigalke,R.D.& Thomas,S.E. 1974. Observations on mortality rates and disease in roan and sable antelope on nature reserves in the Transvaal. J.sth.Afr.Wildl.Manage.Ass. 4(3):203-206

Zimmerman,I. 1980. Predicting diet quality from measurement of nitrogen and moisture in cattle dung. S.Afr.J. Wildl.Res. 10(2):56-60

Appendix 1

Roan antelope body measurements

Roan antelope body measurements were taken during the capture and marking operations. In 1985, management staff took skull length as from the nose to the base of the horns, the standard measurement was taken thereafter. The measurements for adult animals are given below. In Figure 1 the relationship between horn length and basal circumference is shown for males and females of all ages.

Table 1

Body measurements for adult roan antelope

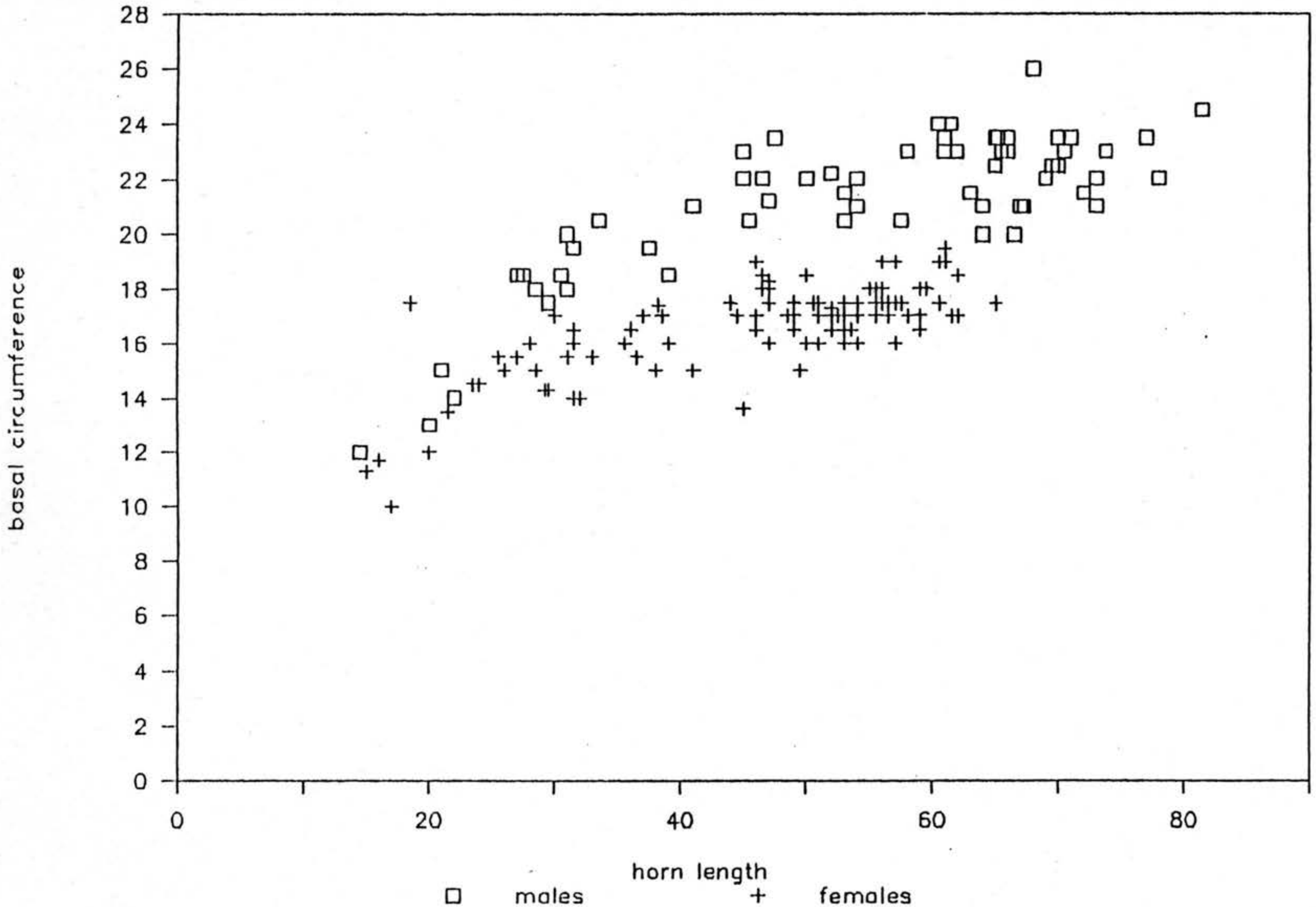
Adult males

	average	STD	Min - Max	N
Horn basal circumf.	22.5	1.1	20 - 24.5	30
Horn length	63.8	9.0	45 - 81.5	30
Tip-tip	26.5	9.4	15.5 - 53	30
Nose to horns (1985)	37.4	2.0	32.5 - 40	11
Skull length	58.7	2.9	53 - 64	19
Horns to base of tail (1985)	180.6	12.2	159 - 199	11
Skull-body	217.8	7.0	205 - 230	19
Tail	48.4	7.9	39 - 76	29
Shoulder height vertical	140.6	28.0	125 - 157	28
Girth	150.6	8.6	134 - 172	29
Ear length	26.9	8.5	25 - 33	23

Adult females

	average	STD	Min - Max	N
Horn basal circumf.	17.3	1.0	13.6 - 19.5	61
Horn length	53.7	5.4	38.2 - 65	62
Tip-tip	22.7	6.1	3.5 - 43	57
Nose to horns (1985)	37.5	1.1	35 - 40	25
Skull length	54.4	2.0	51 - 60	37
Horns to base of tail (1985)	178.1	8.2	158 - 191	25
Skull-body	209.4	9.4	180 -228.5	37
Tail	45.9	6.4	34 - 80	61
Shoulder height vertical	138.4	20.0	128.5 - 152	52
Girth	148.9	8..2	132 - 164	58
Ear length	29.6	1.8	25 - 34	56

Figure 1: The relationship between horn length and basal circumference for males and females of all ages (in cm).



basal circumference
28
26
24
22
20
18
16
14
12
10
8
6
4
2
0
0
20
40
60
80
horn length
males
females

Appendix 2

Waterhole count summary 28-30th June 1988 for roan antelope 48 hours

Waterhole	Total	Juveniles M	F	?	subadults M	F	?	adults M	F	?
Geelhout	71	4	17	4	8	7		8	23	
Huilboom	18	1	4					5	8	
Duitsepos	40	2	3	1	1	1		19	13	
Bergtuin	30	2	5		4	4	1	4	8	2
Securidaca	1								1	
Elandsdrink	25	1	3		3	2		6	9	1
Kiewiet	3							2	1	
Total	188	10	32	5	16	14	1	44	63	3
Subtotal	188		47			31			110	
%	100		25			16.5			58.5	

(79 roan are captured 6-16th July and 2 roan 9th August)

Waterhole count summary 28-30th July 1988 for roan antelope 48 hours

Waterhole	Total	Juveniles M	F	?	subadults M	F	?	adults M	F	?
Geelhout	37	7	5		1	3		5	16	
Huilboom	35	9	6		3	3		4	7	3
Duitsepos	21				1	2	1	9	8	
Bergtuin	20	1	2	6	2			4	5	
Securidaca	9				1	5		1	2	
Elandsdrink	23	1	3		3	4		3	9	
Kiewiet	2							1	1	
Total	147	18	16	6	11	17	1	27	48	3
Subtotal	147		40			29			78	
%	100		27.2			19.7			53.1	

Waterhole count summary 26-29th August 1988 for roan antelope 72 hours

Waterhole	Total	Juveniles M	F	?	subadults M	F	?	adults M	F	?
Geelhout	30	4	5		1	3		5	12	
Huilboom	47	9	10		1	5		12	10	
Duitsepos	29	2	3		1	1		11	9	2
Bergtuin	24	2	5		1	1		5	10	
Securidaca	8				1	1		5	1	
Elandsdrink	18	1	3			4		4	6	
Kiewiet										
Total	156	18	26		5	15		42	48	2
Subtotal	156		44			20			92	
%	100		28.2			12.8			59	

Roan total for 1989

1989 expected total in August

Waterhole	Total	Juveniles			subadults			adults		
		M	F	?	M	F	?	M	F	?
Geelhout	49	2		8	6	10		7	16	
Huilboom	36				7	4		15	10	
Duitsepos	17	2		2	2	3		5	3	
Bergtuin	23	2	1		3	2		4	11	
Securidaca	12			1	1	4		4	2	
Elandsdrink	10			2		1		3	4	
Kiewiet	1							1		
Total	148	6	1	13	19	24		39	46	
%		4	1	9	13	16		26	31	1
%			14			29			57	

1989 What there should be - is based on the count in August and July and my observations on herds/animals seen. The Elandsdrink figure is not very reliable. On the 88/12/19 I counted 12 animals in the Elandsdrink herd together with the radio-collared female. Only 44% of the tagged animals (32 individuals) were identified/counted during the August waterhole count.

1989 observed total in August

Waterhole	Total	Juveniles			subadults			adults		
		M	F	?	M	F	?	M	F	?
Geelhout	49	2		8	6	10		7	16	
Huilboom	36				7	4		15	10	
Duitsepos	11					4		5	2	
Bergtuin	23		3		2			2	4	
Securidaca	12			2	1	1	2	4		2
Elandsdrink	6							3	2	1
Kiewiet	11				1	1		1	8	
Total	136	2	3	10	17	20	2	37	42	3
%		2	2	7	12	15	2	27	31	2
%			11			29			60	

Geelhout - 106 animals were counted all in all. The notes made by the two counters did not allow for a meaningful substraction of duplicates, so that I used the average drinking frequency of 2.33 times for Huilboom (during the same time period) and my July count as basis for the figure of 49 animals.
Huilboom - was counted by myself and apart from 7 males, that came at night, I saw all the roan.

Waterhole count summary 7-9th June 1990
for roan antelope 48 hours

Waterhole	Total	Juveniles			subadults			adults		
		M	F	?	M	F	?	M	F	?
Geelhout	8				6			2		
Huilboom	10				5			3	2	
Duitsepos	12				1	1	1	7		2
Bergtuin	9						3	2	2	2
Securidaca	1									1
Elandsdrink	23	1	1		3			5	13	
Kiewiet	7							4	3	
Total	70	1	1		15	1	4	23	20	5
%			2.9			28.6			68.6	

Waterhole count summary 7-9th July 1990
for roan antelope 48 hours

Waterhole	Total	Juveniles			subadults			adults		
		M	F	?	M	F	?	M	F	?
Geelhout	43	1	2		14	5		9	12	
Huilboom	14				4			6	2	2
Duitsepos	13				1	2		6	2	2
Bergtuin	19							12	7	
Securidaca	5		1					1	2	1
Elandsdrink	17	1	1					3	1	13
Kiewiet	6							4	2	
Total	117	1	3		19	7		41	28	18
%		1	3		16	6		35	24	15
%			4			22			74	

Waterhole count summary 4-6th August 1990
for roan antelope 72 hours

Waterhole	Total	Juveniles			subadults			adults		
		M	F	?	M	F	?	M	F	?
Geelhout	58	3	2		11	6		16	20	
Huilboom	32		2	5	2	5		6	12	
Duitsepos	19				7			9	3	
Bergtuin	18			2	3	2		5	6	
Securidaca	6		1					2	3	
Elandsdrink	21	1	2		1	2		5	10	
Kiewiet	6							3	3	
Total	160	4	7	7	24	15		46	57	
Subtotal	160		18			39			103	
%	100		11.3			24.4			64	

Appendix 3

The population models - an explanation

This appendix explains the working of the two population models. It assumes that the operator has a basic understanding of the spreadsheet program Lotus 123, which was used in constructing these models.

The two models are supplied on the disc, named MODEL_1 and MODEL_2 respectively.
The input parameters that can be changed are printed in bold type in Table 1. In addition the annual captures can be changed in both models and introductions can be changed in Model I.
Both models have several graphs attached, which can be invoked with the command /Graph Name Use. They are as follows:

Model I:

- ADULT_FIT - a graph of adult male and female numbers observed and modeled.
- JUV_FIT - a graph of juvenile numbers observed and modeled.
- J_100F - a graph of juvenile per 100 adult female observed and modeled.
- SUBF_FIT - a graph of subadult male numbers observed and modeled.
- SUBM_FIT - a graph of subadult female numbers observed and modeled.
- TOTALFIT - a graph of population size observed and modeled.

for Model II:

- ADULT_FIT - a graph of adult male and female numbers observed and modeled.
- FEMA_FIT - a graph of subadult and adult female numbers observed and modeled.
- JUV_FIT - a graph of juvenile numbers observed and modeled.
- J_100F - a graph of juveniles per 100 adult female observed and modeled.

STAN_PRO - a graph of population size observed and modeled and projected to the year 2000, using standard input data.

SUBF_FIT - a graph of subadult male numbers observed and modeled.

SUBM_FIT - a graph of subadult female numbers observed and modeled.

TOTALFIT - a graph of population size observed and modeled.

Table 1

The main input tables for population models I and II
(the input variables are printed in bold type)

Waterberg Roan population model
Model I

Starting population		Mortality rate	minimum	observ. pop.	model pop.	year
				70	62	1975
				77	88	1976
Males				**80**	108	1977
Juveniles	**0**	**0.25**		**85**	124	1978
Subadults 1	**0**	**0.3**		**88**	134	1979
Subadults 2	**5**			**100**	148	1980
Adults	**10**	**0.1**	0.083	**141**	179	1981
Females				**176**	201	1982
Juveniles	**0**	**0.25**		**220**	222	1983
Subadults 1	**5**	**0.095**		**275**	246	1984
Subadults 2	10			**210**	206	1985
Adults	**40**	**0.095**	0.083	**245**	225	1986
Total pop.	**70**			**215**	215	1987
				156	157	1988
Fecundity	**0.92**	max. 1.2		**150**	160	1989
				160	173	1990
					190	1991
					210	1992
					230	1993
					251	1994
					274	1995

Waterberg Roan population model
Model II

		Mortality rate	minimum	year	rain	observ. pop.	model pop.
				1984	**219**	**275**	275
				1985	**73.3**	**210**	224
Males				1986	**78.7**	**245**	232
Subadults 1		**0.3**		1987	**142.7**	**215**	213
Subadults 2				1988	**142.8**	**156**	159
Adults		**0.1**	0.083	1989	**164.9**	**150**	165
				1990	**35.8**	**160**	165
Females				1991	**112.8**		188
Subadults 1		**0.095**		1992	**114.4**		209
Subadults 2				1993	**114.4**		226
Adults		**0.095**	0.083	1994	**114.4**		247
Total pop.				1995	**114.4**		270
				1996	**114.4**		294
Juvenile : 100 Female				1997	**114.4**		321
ratio change factor	**1.45**			1998	**114.4**		349
starting year	**1991**			1999	**114.4**		381
model avg. ratio is	53.0			2000	114.4		415
range is	33.7	to	63.0				