Challenges faced in the conservation of rare antelope: a case study on the northern basalt plains of the Kruger National Park

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The conservation of rare antelope has long been one of the goals of the Kruger National Park. The roan antelope *Hippotragus equinus*, and to a lesser extent the tsessebe *Damaliscus lunatus*, represent low-density species or rare antelope in the park. Specific management approaches representing the older equilibrium approach, have been employed to conserve these antelope. Of these, the supply of artificial water over many decades was the most resource intensive. The sudden, severe drop in the roan antelope population towards the end of the 1980s was unexpected and, retrospectively, attributed to the development of a high density of perennial waterpoints. The postulated mechanism was that the perennial presence of water allowed Burchell's zebra *Equus burchelli* to stay permanently in an area that was previously only seasonally accessible. The combined effect of a long, dry climatic cycle, high numbers of zebra and their associated predators was proposed to be the cause of this decline. As part of the new nature evolving or ecosystem resilience approach, twelve artificial waterpoints were closed in the prime roan antelope habitat in 1994 in an attempt to move the zebra out of this area. The zebra numbers declined as the rainfall increased. Closure of waterholes clearly led to redistribution of zebra numbers on the northern plains, zebra tending to avoid areas within several kilometres of closed waterpoints. However, at a larger scale, regional densities appeared similar in areas with and without closed waterpoints. There was an initial drop in the lion numbers in 1995, after which they stabilised. In spite of an improvement in the grass species composition and an increase in biomass the roan antelope population did not increase. The complexity of maintaining a population at the edge of their distribution and the problems associated with the conservation of such populations are discussed in terms of management options and monitoring approaches that may be employed in this process.

Key words: artificial waterpoints, management, predation, drought, zebra, rare antelope.

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Introduction

In a review of the large mammal distribution and status in the Kruger National Park (KNP), Pienaar (1963) described the roan antelope as one of the few species that had not reacted favourably to conservation actions. The population of roan antelope *Hippotragus equinus* had oscillated between 150 and 300 over about 60 years since the proclamation of the Kruger National Park. Sable antelope *Hippotragus niger* were found to be very susceptible to drought conditions and tsessebe populations *Damaliscus lunatus* were only growing favourably in the area north of the Letaba River at the time of this review. These species have received special

Table 1

Summary of two management approaches the nature balanced pre-1994 and nature evolving post-1994(Holling & Gunderson 2002). Most of these were employed over the whole KNP, although the effects on the northern basalt plains (NBP) is emphasised especially for the post-1994 period

Management option	Management action pre-1994	Expected outcome
Water provision	To animals whose migration routes out of the KNP were cut off by fencing (Pienaar 1985).	Stabilising numbers of migrating animals especially zebra and wildebeest.
	In forage-rich areas that would otherwise be inaccessible to water-dependent species (Pienaar 1963).	Wider utilisation of available forage and an increase in herbivore numbers.
	As a tool to increase and stabilise numbers of rare antelope (Nature Conservation Year Report of 1961/1962 (Anon 1962)	Increase and stabilisation of numbers of rare antelope.
Disease control	Roan antelope vaccinated against anthrax 1971 – 1992 on the NBP only (De Vos *et al*. 1973)	Decrease losses of roan antelope due to anthrax epidemics.
	The first boundary fence was erected in 1957 and the last elephant proof fence was completed in 1976.	Fence to keep diseases out and to avoid diseases being transferred to domestic stock (Joubert 1986).
Fire	No management fires till 1912	Provide green grazing for animals.
	Biennial burns till 1946	
	Five yearly burns till 1958	
	Triennial burns till 1970	
	According to biomass till 1992 (Van Wilgen *et al.* 2000)	
Animal control	Carnivore control at various stages 1912 to late 1920s, late 1940s to 1961, mid 1970s (when the zebra and wildebeest numbers dropped severely) (Joubert 1986).	To allow herbivore numbers to increase.
	Zebra and wildebeest culled in 1960s (Joubert 1986).	To avoid overutilisation of the vegetation during low rainfall years.
	Culling of buffalo 1966 – 1991.	To avoid overutilisation of the vegetation.
	Culling of elephant 1967 – 1994.	To avoid overulitlisation of the vegetation.

Water provision / .....

Table 1 *(continued)*

Management option	Management action post 1994	Expected outcome
Water provision	Close 12 waterpoints on the NBP (Grant 1999)	Zebra will move out of the area. This will allow an increase in roan antelope due to improved vegetation. Predators will decrease following the decline in zebra
Disease control	Stopped anthrax vaccination in 1991	Decrease the splitting of the roan antelope herds in response to the darting and hence enhance the growth of the population
	Western boundary opened in the south of the KNP	A larger area available to the rare antelope may enhance their populations
Fire	Start with a patch mosaic burning system in 2002 (Van Wilgen *et al*. 2000)	Provide green forage to tsessebe and sable (Gureja 2001)
Animal control	Stopped all culling in 1998 (elephant are still being removed)	Animal populations will settle at optimal densities for the landscape and rainfall.
	Second enclosure was built in 2002.	This will increase the breeding potential of the captive roan antelope and thus the number that can be released in a group (Grant & Van der Walt 2000).

attention from management since 1963 (Grant & Van der Walt 2000).

The different scenarios that could have led to the poor population growth of the roan antelope were discussed in detail in the Nature Conservation Year Report of 1961–1962 (Anon 1962). The unsuitability of the habitat was cited as the most likely limitation to population growth. Disease, specifically anthrax, and a decrease in the vitality of animals due to inbreeding were also mentioned, as was the possible role of predation.

Roan antelope in the KNP have always been concentrated on the northern basalt plains (NBP) at the northeastern tip of the park. A substantial herd of 10–20 roan antelope was also present in the southern granites in the Pretoriuskop area from 1960 to 1985, according to ranger reports. The area to the north of the NBP has some species more characteristic of the mesic savannas, such as nyala *Tregalaphus angasi* (Pienaar 1974), which commonly occur along large drainage lines and rivers. Seasonal rivers and the broad, marshy drainage lines form corridors connecting the NBP to similar habitats to the north and east. These low-lying areas mostly consist of dambo-like grasslands similar to the habitats utilised by roan antelope and tsessebe in Mozambique and Zimbabwe (Joubert 1976). Smithers (1983), states that the habitat requirements of tall grass cover and available surface water are essential to roan antelope and their occurrence is confined to areas with suitable habitat. Tsessebe

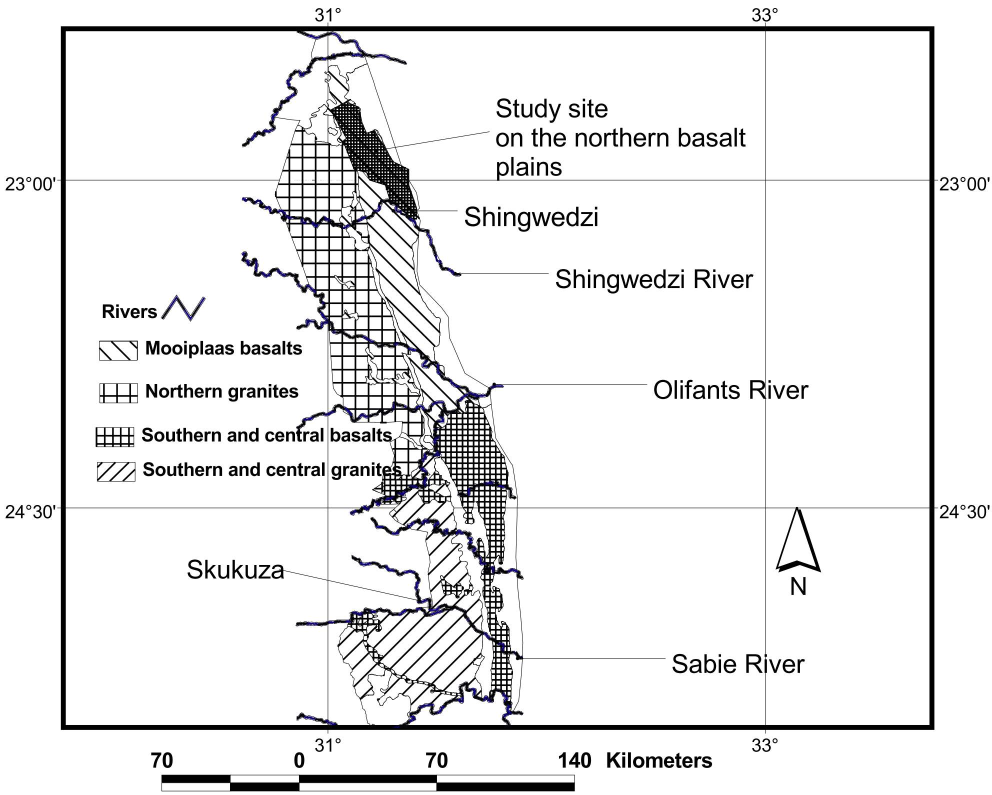

Fig. 1. Location of geographical zones in the granite and basalt landscapes relative to the main rivers.

generally prefer short grassland (Child *et al.* 1972; Joubert & Bronkhorst 1977) and are attracted to the green shoots appearing after fires in the presence of sufficient soil moisture (Garstang 1982). Tsessebe are highly dependent on surface water within open woodland. Bush encroachment accounts for reductions in their range and numbers (Smithers 1983). Tsessebe, and to a lesser extent, roan antelope, show a specific preference for the more open ecotones between the tall woodland and the open grassland of the vleis (Joubert 1970). The ecotone area also forms an important forage area for the large variety of other grazers that occur in the area, of which Burchell's zebra *Equus burchellii* and buffalo *Syncerus caffer* make up the largest percentage (Pienaar 1963). Sable antelope are a savanna woodland species, dependent on cover and availability of water (Smithers 1983), preferring the *Combretum/Mopane* woodland with high trees and large canopies in the granitic western half of the KNP (Pienaar 1974).

The Nature Conservation Year Report of 1961–1962 (Anon 1962) discusses possible management approaches to enhancing the roan antelope population and provides a good illustration of the equilibrium resilience approach (Holling & Meffe 1996) of the time. These were supplementation of the KNP roan from Namibia, the development of dams along the eastern border to attract some of the remaining large roan herds from the adjacent part of Mozambique,

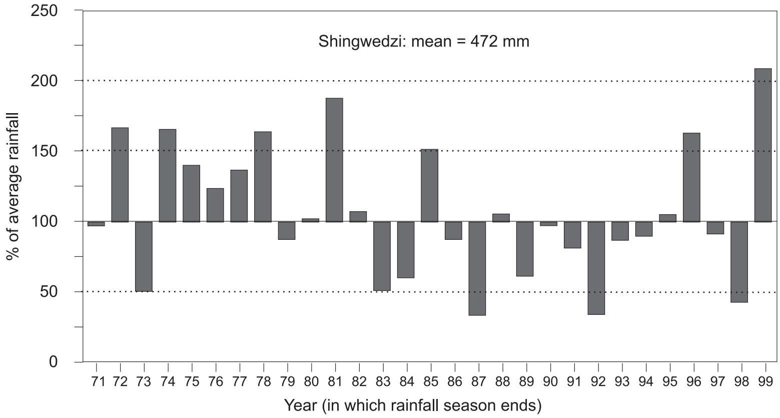

Fig. 2. Percentage deviation from average rainfall at Shingwedzi between 1971 and 1999. Year on X-axis is the year the rainfall season ends 30 June.

and the creation of more suitable habitat by clearing the drainage lines of mopane trees.

This paper aims at providing an historical overview of management approaches used in the KNP and northern basalt plains (NBP) from 1960 to 2000, and the associated changes in animal numbers and vegetation. The definition of Holling & Gunderson (2002) of two basic management approaches is used (Table 1).

1. A structurally static view of "nature balanced", which concentrated on conserving the elements of the ecosystem by assuming overall equilibrium (Holling & Meffe 1996). This approach was followed from about 1960 to 1994 (Joubert 1985). We postulate that as predicted by Holling & Meffe (1996) this approach led to a reduction in the resilience of the system as a result of limiting natural variation.
2. From 1994 onwards, the more dynamic view of "nature evolving" was adopted (Braack 1997) and was aimed at conserving the ability to adapt to change, thus "creating options to buffer disturbance and to create novelty". Only the initial results of this approach on the NBP of the KNP are discussed here. As part of this discussion; the importance of monitoring and adaptive management are highlighted.

Although it is true that management was adapting their approach before 1994, this year was taken as the dividing line because it was then that the first consciously "destabilising" management action was taken (one promoting variability), viz., the closing of waterpoints

Study area

The Kruger National Park is coarsely divided longitudinally into basaltic (eastern) and granitic (western) zones (Gertenbach 1983), and the vegetation is broadly defined as an arid/eutrophic savanna (Huntley 1982). The area north of the Olifants River is dominated by mopane, while the vegetation in the southern half of the park consists mainly of broad-leaved *Combretum* species on the granite crests and Acacias in the valleys. The southern basalts are dominated by knobthorn *Acacia nigrescens* and marula *Sclerocarya birrea* (Fig. 1). The study area of the NBP stretches over an area of 700 km² with the Shingwedzi River in the south, the Punda hills in the north, the basalt/granite division in the west, with the Nwambiya sandveld in the east. The vegetation is classified as Mopane (*Colophospermum mopane*) shrubveld on basalt (Gertenbach 1983). For comparative purposes, the KNP is divided into four granitic and four basaltic zones, with the large rivers (Shingwedzi, Olifants and Sabie) forming the zone boundaries (Fig. 1).

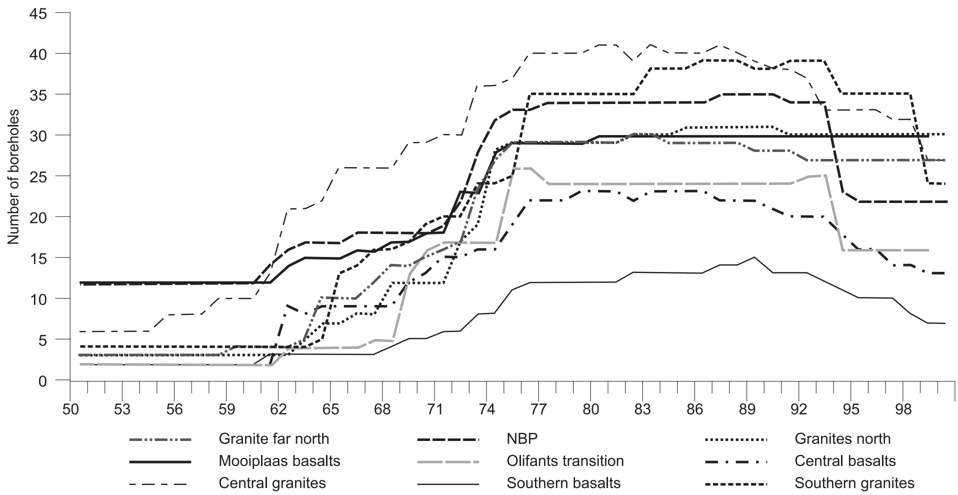

Fig. 3. Development of waterpoints in different geographical zones between 1950 and 2000.

This summer rainfall area has a mean annual rainfall of 477 mm north of the Olifants River, measured over 32 years at 10 rainfall stations, and 560 mm south of the Olifants River measured at 12 rainfall stations over 46 years (Zambatis & Biggs 1995). In Fig. 2, the percentage deviation from the mean annual rainfall is shown at Shingwedzi over the station's recording period. At Shingwedzi, a wet cycle occurred in the seventies followed by a drier cycle in the eighties and nineties. Here the average rainfall decreased from 551 ± 65 mm between 1977 and 1986 to 338 ± 60 mm between 1987 and 1993, with 344 ± 76 mm between 1994 and 1998. The mean KNP rainfall was also significantly higher during the period 1977 to 1986 (561 ± 18 mm) than between 1987 and 1993 (423 ± 18 mm) and between 1994 and 1998 (357 ± 39 mm) ($p < 0.0005$).

Development of waterpoints

During the four decades between 1939 and 1980 there was a steady increase in artificial water supply, with the largest number of windmills erected between 1960 and 1980 (Fig. 3). On the NBP a total of 35 active boreholes plus six dams were established by 1975. This development resulted in a significantly higher density of waterpoints on the NBP than all the other areas over 18 years ($p < 0.0005$) with an average of 41 km² per borehole over that period. The density of boreholes present in 1986 at the start of the roan antelope decline in the different geographical zones is listed in Table 2.

Closure of waterpoints

During 1994, 12 waterpoints were closed, over an area of 412 km² in the northern part of the NBP, where the only remaining roan herds were left. The windmills in a comparative area of 360 km² to the south remained open. One critically placed dam was breached in June 1996. In March 1998 another waterpoint further south was closed, and in March 1999 another two.

Fences

The boundary fences precluded any movement of animals from or towards habitats in

Table 2

The area of the different geographical zones and the density of boreholes in 1986

Description	Size in km²	Borehole density in km²/borehole in 1986
Far northern granites	1777.4	62
Northern basalt plains (NBP)	1328.1	37
Northern granites	2003.1	68
Mooiplaas basalts	1838.5	61
Olifants transition zones	1791.4	74
Central basalts	3001.9	132
Central granites	2570.1	64
Southern basalts	1739.7	140
Southern granites	1811.7	50

Mozambique and Zimbabwe where roan antelope, sable antelope and tsessebe were once common (Anon 1962). Thus within the KNP the rare antelope were restricted to the southern boundary of their distribution. Anecdotal information provided in a report by the Park Biologist (Anon 1961) indicate that there was movement across the KNP boundary before the fences were erected, some of the roan herds further south being split by the western boundary fence.

In 1995, the south-western boundary fence between the KNP and the private reserves was removed, and in 2002, negotiations to remove the fence between the north-eastern border of the KNP and Mozambique were finalised (Gaza-Kruger-Gonarezhou Transboundary Natural Resources Management Initiative 2002).

Anthrax vaccination

Anthrax caused the death of at least 83 roan antelope (over 11 years, during epidemics in 1959, 1960 and 1970) out of an estimated mean population of 250 north of the Olifants River (De Vos *et al*. 1973). During the same period only eight sable were recorded to have died of anthrax. Anthrax was thus identified as a major threat to the small roan population and the decision was taken to vaccinate them. Roan antelope were immunised annually between 1971 and 1992, on the NBP, but not on the Mooiplaas basalts which were further from the main focus of infection along the Levuvhu River. Projectile syringes were used from 1971 until 1984, after which bio-bullets were used. Vaccination was stopped in 1992 because it was believed that the immunisation procedure scattered the few remaining roan herds and made them more vulnerable.

Roan enclosure

Because of the possibility of losing all the roan antelope in the park, seven roan antelope including three males (one adult) and four females (two adult) were placed in the existing N'washitshumbe enclosure between June and August 1994. A single calf was born in December 1994. This enclosure of 254 ha (which excludes large predators and all other herbivores) was erected roughly in the centre of the NBP in 1967 (Joubert 1970) and expanded in 1986 with 48 ha to include a part of the adjacent watercourse and associated ecotone vegetation.

Initiation of a specific research programme (northern plains programme).

This programme was initiated in 1994 and aimed at evaluating the effects of the closure of waterpoints (Harrington & Pienaar 1994). It was postulated that the decline in roan antelope was related to the increase in the zebra population that was responding to an increased density of artificial waterpoints, and that predation of adult roan antelope also played a significant role in the decline (Mills *et al*. 1995a; Owen-Smith 1996; Harrington *et al*. 1999). The initial studies thus concentrated on the effect of closure of waterpoints on vegetation, roan antelope, zebra and lion *Panthero leo* populations.

Monitoring

Aerial census

From 1980 until 1994, a fixed-wing aircraft was used to provide a total aerial coverage of the KNP between May and August every year, using four observers. From a height of 65–70 m above ground level, parallel strips of about 800 m wide (400 m each side) were flown (Viljoen 1996), covering the entire Kruger National Park. On the NBP this census was continued between 1994 and 1998 while only incomplete census counts were done in the rest of the KNP. In 1999 and 2000 a 50 % sample of the NBP and a 17 % sample of the rest of the KNP was counted using the Distance sampling method (Buckland *et al*. 1993).

Buffalo counts were done using a helicopter, by splitting herds into smaller groups and then photographing them. Animals on the photographs were then counted with visual aids.

Vegetation condition assessment

Range condition has been assessed yearly at 18 specific localities on the NBP since 1989, using a standard range condition assessment (VCA) technique (Trollope *et al*. 1989; Trollope 1990). At each point the grass species were recorded, and the frequency of each species was expressed as the percentage of the total number of grasses. Grasses were grouped into decreasers (grasses that decrease with intense utilisation by herbivores) and increasers (species that increase with intense utilisation by herbivores).

Fifteen new VCA localities were added on the NBP in 1994 to increase the sampling intensity in the area where the waterpoints were closed.

Forage utilisation by roan antelope

Roan antelope were located by radio-tracking between March and October 1996. Starting at the point where they were recently found to be grazing, a standard range assessment (Trollope *et al*. 1989) was done at 60 sites along four diagonal transects of 15 m each in quadrats of 20 cm^2. In addition to the standard measurements, leaf height, compressed height as determined with the disc pasture meter, grass species utilised, and percentage utilisation was recorded.

The effect of artificial waterpoints on surrounding vegetation

The effect of the presence of artificial water on the surrounding vegetation was examined by comparing the vegetation in the area of open windmills to that in the area of closed windmills. Recovery of the herbaceous layer was aimed at determining how the herbaceous layer around three artificial waterpoints improved after decreasing herbivore pressure, brought about by the closure of the waterpoints (Davidson 1996). This study was expanded to look at the spatial structure of the herbaceous vegetation under different grazing intensities, as well as the species association (Jacoby 1999). A further study was undertaken to examine changes in woody composition around waterpoints. For this study vegetation was examined around four open waterpoints, and four closed (Fruhauf 1997).

Herbivore studies

Rare antelope studies

Studies on roan antelope (Joubert 1976), tsessebe (Joubert 1972) and sable (Joubert 1976) were undertaken to establish their habitat preferences. Joubert (1970) investigated the social behaviour of roan antelope.

In 1994, two cows in each of the two largest roan antelope herds were fitted with radio collars. Once a signal was detected from an elevated point, the animal was followed by vehicle and its position recorded. The distance to the nearest waterpoint, and the position in the landscape according to the land unit classification (Venter 1990) was also recorded. As far as possible, the number, sex, and age-class distribution was determined for each located group or herd. Due to poor visibility the whole herd was often not seen, and some young calves could have been missed.

Monthly reports of rangers with observations of rare antelope were used for data up to 1984, after which data came from Mason (1990) up to 1990. No data is available for 1990–1994.

Zebra observations

Zebra activity and position in the landscape was noted when they were encountered during roan radio-tracking sessions. In the case of zebra, the position in the landscape was recorded in only two categories—upland and lowland.

Thirty zebra females from separate herds in the study area were fitted with colour-coded collars in November 1993. Visitors and staff members, whose

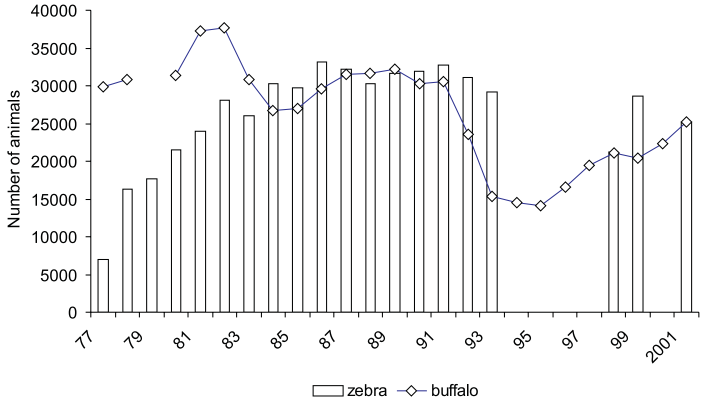

Fig. 4. Zebra and buffalo numbers in the KNP from total aerial counts for buffalo and for zebra between 1977 and 1993. (Counts between 1998 and 2001 are estimated from a 17 % and 22 % sampling, respectively, according to the Distance procedure (Buckland et al. 1993).

involvement was encouraged by posters, recorded sightings of collared zebra on forms that were placed in the reception area of major rest camps.

Predator studies

Lion census

In order to determine lion densities, the mass capture technique of Smuts *et al*. (1977a, 1977b) was employed to attract lions to calling stations in 1989. This census was repeated in 1993, 1996, 1998 and 2002, with slight changes in the locality of the survey points. The area covered by this census technique is not constant as lions are drawn from territories outside the designated study area. Also, no statistical tests can be used to compare surveys (Mills *pers. comm.*).

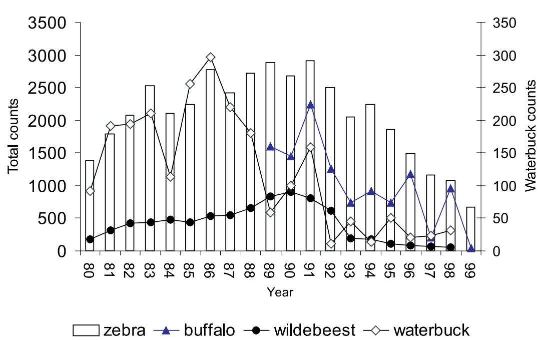

Fig. 5. Numbers of common herbivores on the northern basalt plains from total counts between 1980 and 1999.

Data analysis

Herbivore numbers

Animal counts and densities at different periods and in different geographical zones were normalised for statistical analysis by natural logarithms. Animal populations in different areas were compared in a multiple ANOVA, correcting for the effect of rainfall by including the annual rainfall for each geographical zone as covariate. Standard error is presented in brackets in tables and text.

Area per animal and area per borehole were calculated by dividing the area size by the number of animals or boreholes.

Roan herd totals, according to ranger reports, Mason's reports, and data collected by the research programme since 1994, were grouped as follows: 1950-1964; 1965-1969; 1975-1985; 1985-1994; 1986-1994; and 1995-2001.

Vegetation

The chi-square test was used to test the difference in abundance of species on the VCA plots compared to the areas where roan ante-

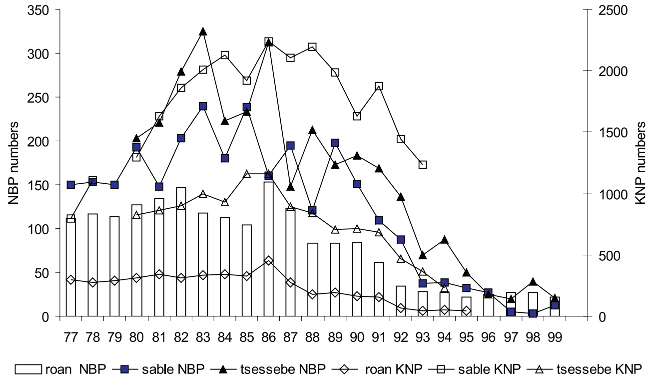

Fig. 6. Rare antelope numbers in the KNP between 1977 and the last total aerial census in1995 and on the NBP between 1977 and 1999. Bars are roan on NBP; solid symbols are rare antelope on NBP; open symbols are rare antelope in KNP.

lope preferred to graze. The selection of specific habitats by roan antelope compared to the general area covered by each habitat as estimated in Venter's (1990) land unit classification was tested in the same way.

Differences in vegetation condition parameters between geographical zones north of the Olifants River were determined in a multiple ANOVA using standing crop as indicator of biomass and percentage of decreasers and increasers as indicators of forage quality. Percentage of decreasers and increasers were normalised, using the square root arcsine transformation. To test the effect of the closure of waterpoints on the vegetation condition parameters, the 1999 VCA results were corrected for the 1994 situation by using the 1994 data as a covariate.

Table 3

The mean density in the geographical zones between 1980-1993 of zebra in the KNP and the density of rare antelope north of the Olifants River (Standard error in brackets)

Zone	*n*	km²/zebra	km²/roan	km²/sable	km²/tsessebe
Far northern granites	13	0.84 ^{abC} (0.07)	186 ^{ab} (74)	8.09 ^{A} (13.8)	61.96 ^{ab} (41.8)
Northern basalt plains	22	0.67 ^{aB} (0.07)	22 ^{A} (57)	13.5 ^{aB} (11.4)	14.5 ^{aB} (32.1)
Northern granites	19	0.99 ^{abC} (0.07)	190 ^{abC} (61)	7.4 ^{A} (11.38)	55 ^{ab} (34.5)
Mooiplaas basalts	19	0.56 ^{B} (0.07)	35 ^{aB} (61)	67.9 ^{abc} (11.39)	5.5 ^{A} (34.6)
Olifants transition zone	18	0.60 ^{B} (0.07)		21.9 ^{abC} (11.7)	
Central basalts	16	0.51 ^{A} (0.074)			
Central granites	16	0.48 ^{A} (0.074)			
Southern basalts	16	1.39 ^{abc} (0.076)			
Southern granites	16	1.69 ^{abc} (0.074)			
Significance within column		$p < 0.0005$	$p < 0.0005$	$p < 0.0005$	$p < 0.0005$
Significance of rainfall as covariate		$p < 0.0005$	$p = 0.003$	NS	NS

Letters in superscript and upper case indicate a significant difference with the same letter in superscript and lower case. Thus value ^{A} differs significantly form value ^{a} in the same column.

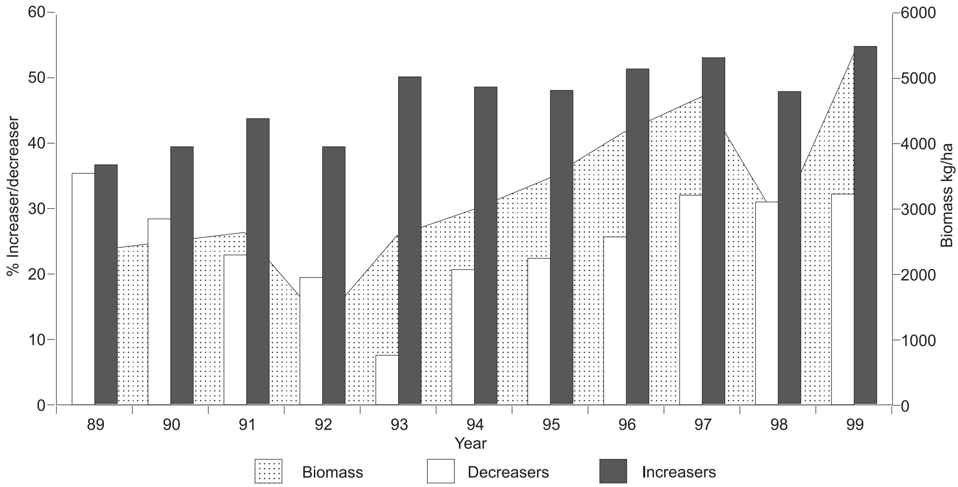

Fig. 7. Changes in biomass (standing crop) and percentage palatable, perennial decreaser species between 1989 at the start of the vegetation surveys and 1999.

Results of management strategy up to 1994

Herbivore numbers

Zebra numbers in the KNP showed a steady increase since 1977 when the aerial counts started, levelling off after 1985. The buffalo population was fairly stable due to culling and then declined sharply after the 1991 drought (Fig. 4). There was a corresponding steady increase in the zebra population on the NBP until 1991, a year in which rainfall was very low (Fig. 5). The population of blue wildebeest *Connochaetes taurinus* did not increase as much as the zebra, and

Table 4
Difference in vegetation parameters in 1994 in the different geographical zones n = *435*

Geographical zone	Biomass kg/ha	% decreasers	% increasers
Far northern granites	1935 [Ac]	13.73 b	85.2 [ABC]
Northern basalt plains	3002 [ABC]	22.6 [AB]	66.5 [Ac]
Northern granites	739 [a]	6.8 [a]	90 [ABC]
Mooiplaas basalts	1191[a]	12.96 b	83.1 [ABC]
Olifants transition zone	736 [a]	10.3 [a]	82 [ABC]
Central basalts	1865 [Ac]	17.72 [Ac]	71.7 [Ac]
Central granites	1743 [Ab]	19.25 [Ac]	65.8 [Ab]
Southern basalts	2389 [AB]	23.43 [AB]	71.5 [Ac]
Southern granites	1926 [Ac]	26.28 [ABC]	54.3 [a]

Letters in superscript and upper case indicate a significant difference with the same letter in superscript and lower case. Thus value [A] differs significantly form value [a] in the same column.

Biomass (p = 0.0000), percentage decreaser species (p = 0.0000) and percentage increaser species (p = 0.000) differed significantly.

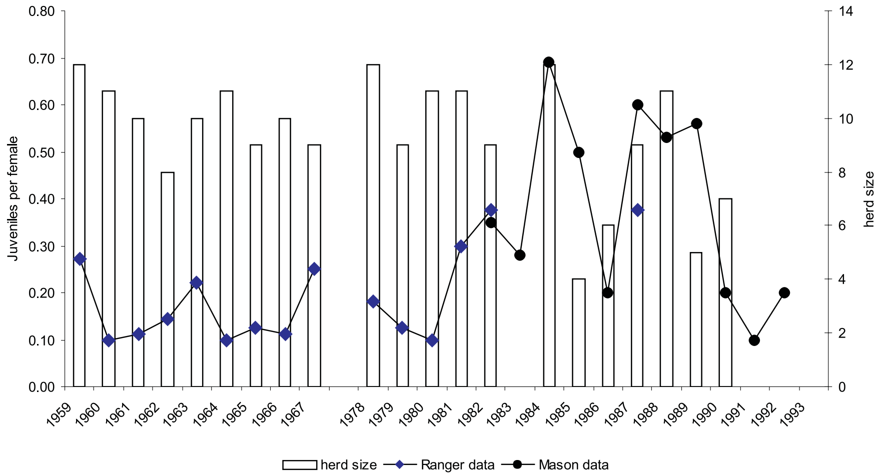

Fig. 8. Herd size of roan antelope (bars) and juvenile to adult female ratios (line) in the northern KNP from 1984 to 1999 for two sets of data.

decreased substantially after 1991. The buffalo population on the NBP showed wide fluctuations due to movement in and out of the study area, high numbers being present during the census period in 1991. The numbers of the strongly water-associated waterbuck *Kobus ellipsiprymnus* varied with the rainfall, but stayed low after the 1991–1992 drought. Sable, tsessebe and especially roan antelope declined dramatically since 1986 in the Kruger National Park. Even in the south where the dry season rainfall is generally higher (Zambatis & Biggs 1995), the Pretoriuskop herd disappeared in 1985. This decline was as evident in the NBP, the prime habitat of roan antelope and tsessebe (Fig. 6), although the NBP still remained one of the areas with the highest rare antelope populations (Table 3).

Overall the high zebra numbers did not show the expected negative correlation with the roan antelope population; indeed there was a small but significant positive correlation (r = 0.18, n = 168, p = 0.018) between roan numbers and zebra numbers in different zones of the park. On the NBP, this relationship seemed numerically stronger but not significant (r = 0.31, n = 31, p = 0.08).

Vegetation

The northern and southern basalts had the highest biomass. Percentage decreasers were the highest in the southern granites and basalts, and in the northern basalts (Table 4). The low rainfall in 1992–1993 resulted in the lowest recorded biomass and percentage decreaser species (Fig. 7).

Disease management

The effect of vaccination was examined by looking at the density of roan antelope numbers on the plains, compared to the density in the adjacent Mooiplaas basalts, where the roan were not vaccinated at any stage. The density of roan antelope on the NBP of 14.8 (± 40) km²/roan between 1980 and 1992 did not differ significantly from the 28 (± 40) km²/roan in the Mooiplaas basalts during this vaccination period. The density of roan antelope after the decline between 1993 and 1995 did not differ significantly. The density was 51 (± 58) km²/roan after vaccination stopped on the NBP, versus 98 (± 82) km²/roan on the Mooiplaas basalts.

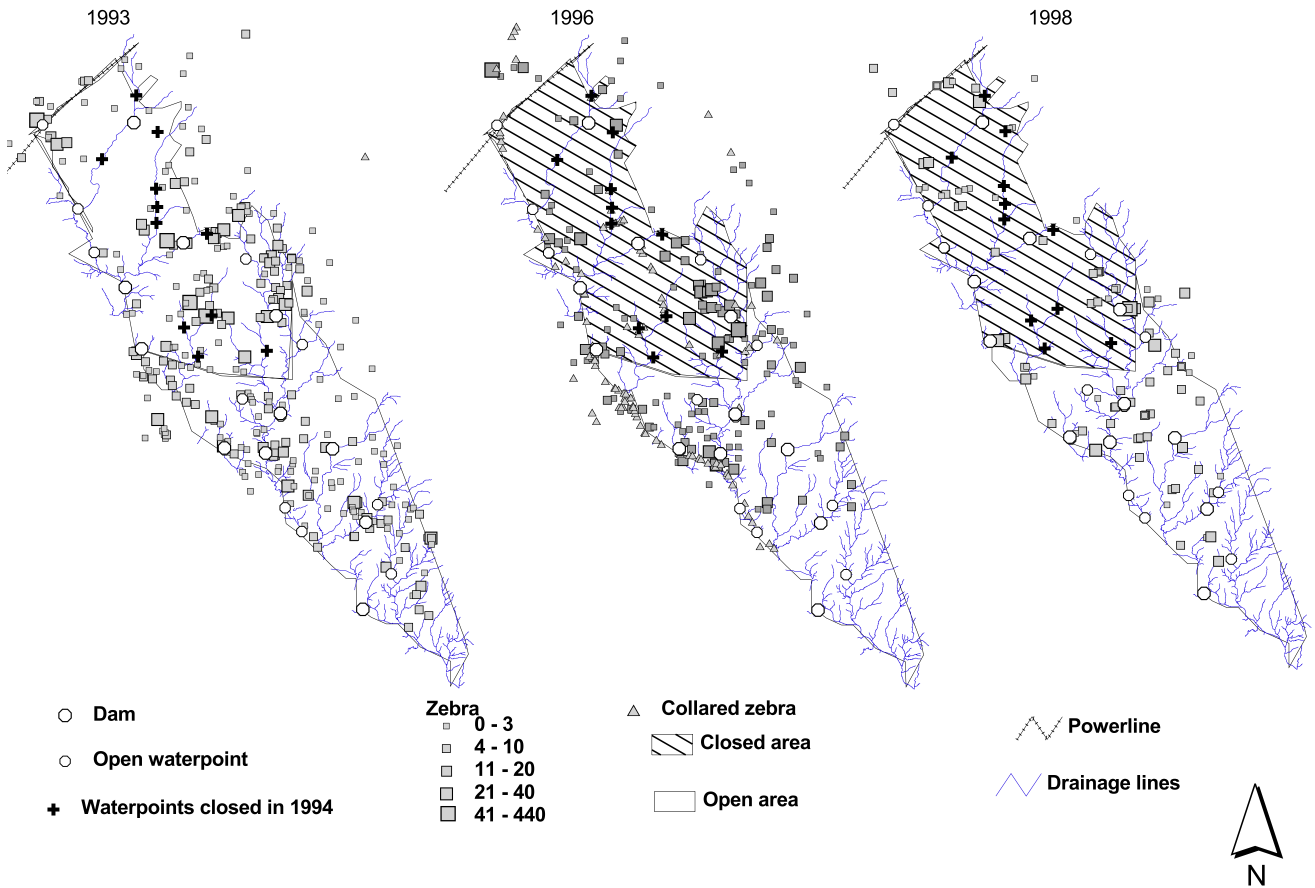

Fig. 9. Distribution of zebra in 1993, before closure of waterpoints in 1994. The subsequent movement away from the central area where waterpoints were closed is illustrated—two years after closure in 1996 and four years after closure in 1998. The movement of colour-collared zebra towards the south is indicated on the 1996 map.

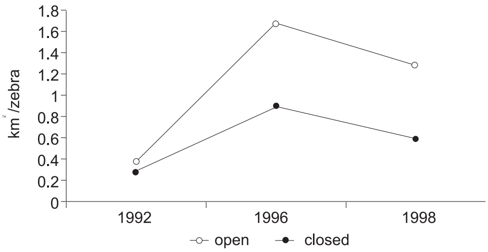

Fig. 10. Density of zebra in the open and closed area of the northern plains.

Rare antelope

On the plains, the number of breeding herds of roan antelope—with more than six individuals per herd—had decreased from four in 1970 (Joubert 1970), to two in 1984. Herd sizes differed significantly between the approximate ten-year periods since 1957 ($p = 0.003$). The largest average herd size in this area was 9.4 (Fig. 8) in the north, recorded between 1980 and 1985, while the average was 8.8 between 1957 and 1964, and 6.3 between 1986 and 1994.

The juvenile to adult female ratios of the roan antelope were very high between 1984 and 1989, but then decreased to levels recorded before 1984 (Fig. 8).

Results of management actions after 1994 on the northern basalt plains

The effect of waterpoint closure on the herbivores

There was a general decline in herbivores on the NBP that, however, started before the closure of waterpoints in 1994 (Fig. 5). Thus the total number of herbivores (zebra, buffalo, wildebeest and waterbuck) counted (2573 ± 458) between 1995 and 2000 is significantly less than the numbers of these her-

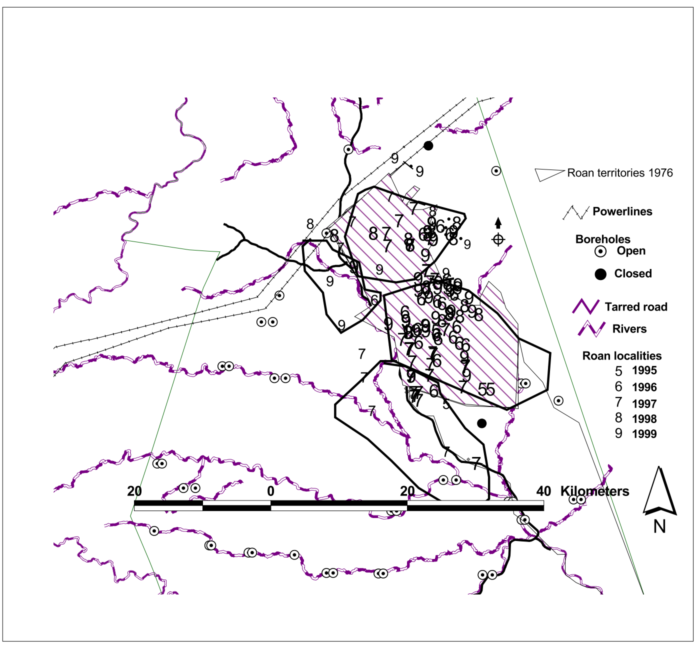

Fig. 11. The relation of open and closed waterpoints on the NBP to the distribution of radio-collared roan antelope between 1995 and 1999, and the activity zones described in 1976.

bivores on the NBP between 1980 and 1994 (6552 ± 348) ($p < 0.0005$) (Fig. 5).

Zebra continued their decline with the increase in rainfall, as expected (Mills *et al.* 1995), and moved away from the core area where waterpoints were closed towards the open waterpoints and concentrated along drainage lines (Fig. 9). However, the decline in the open and closed areas was very similar (Fig. 10). Tsessebe populations declined sharply after closure of waterpoints in 1994, from 98 on the NBP in 1993, to between 20 and 40 in 1998 (Fig. 6). During the same period the sable decreased from 60 in 1993, to 3 in 1998 (Fig. 6), probably due to movements westward to the granites. The roan antelope population stabilised at about 21 animals after 1994, but did not increase (Fig. 6).

Positions where radio-collared roan antelope were recorded during the study period mostly fell within the home range boundaries of territories established by Joubert (1976). Very few animals were sighted in the southern part where waterpoints were still open (Fig. 11). Furthermore, the herd of 20 roan antelope that was recorded in 1981 near the Langtoon dam (in the south-eastern corner of the closed area) with a permanent zebra herd, had declined to only five animals in 1994, and disappeared towards the end of 1997.

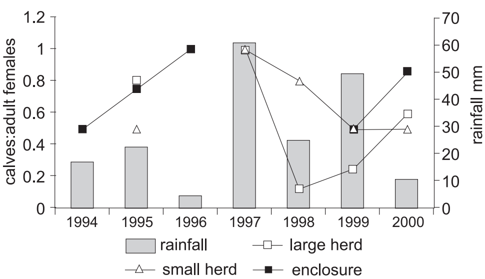

Fig. 12. Calves produced per cow in the free roan antelope herds as well as in the N'washitshumbe enclosure, compared to the dry season rainfall.

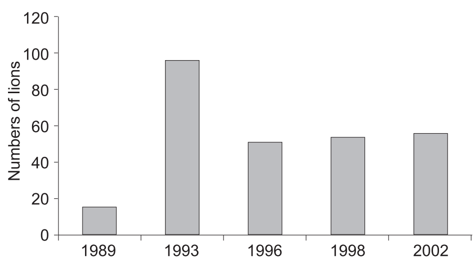

Fig. 13. Lion numbers on the northern basalt plains.

Table 5
Selection of habitats by roan relative to the area covered by the land type

Habitat	% roan encounters	Habitat as % of Mooiplaas land type[a]
Crest	35	77
Midslope	25.8	10
Low lying area	19.5	7
Drainage lines, vleis and ecotones	19.5	6

[a]According to Venter (1990).

Growth of population in the N'washitshumbe enclosure compared to that in the free-ranging herds.

The number of the animals in the enclosure increased from 7 in 1994 to 39 in May 2001. The breeding herd in the enclosure then consisted of: 1 adult bull; 7 adult cows; 4 young animals 20–30 months old; 5 calves of 10–12 months; and 8 calves of 6 weeks; the other 14 animals did not form part of the breeding herd.

The animals in the enclosure showed a steady increase, in contrast to the free-ranging population. There did not seem to be a link between the dry season rainfall (July to September) of each year and the population growth or the number of calves per cow produced in the enclosure or outside as suggested by Owen-Smith & Ogutu (*in press*) (Fig. 12).

Table 6

Difference in vegetation in the areas north of the Olifants River in 1999 correcting for the vegetation status of 1994

	Biomass			% decreasers		
Geographical zone	kg/ha	*sd*	n	%	*sd*	n
Far northern granites	1898 ^{aB}	163	41	14.4 ^{a}	2.5	35
Northern basalt plains	2970 ^{A}	148	50	22.3 ^{A}	2.2	47
Northern granites	772 ^{ab}	157	44	7.9 a	2.3	41
Mooiplaas basalts	1167 ^{abC}	142	54	12.7 ^{a}	2.0	52
Olifants transition zone	735 ^{abc}	155	45	10.5 ^{a}	2.2	6.1

Letters in superscript and upper case indicate a significant difference with the same letter in superscript and lower case. Thus value^{A} differs significantly form value^{a} in the same column. (Biomass (p = <0.0001); percentage decreaser species (p <0.0001).

Overlap in habitat selection of roan antelope and zebra

The mean home range of nine colour-collared zebra calculated from 487 sightings, between November 1993 and May 1995, was 267 ± 103 km². This is much larger than the home range calculated for the four radio-collared roan antelope (60 ± 4.5 km²). Zebra home ranges thus include more waterpoints than those of the roan antelope, which restrict their movements to one or two waterpoints.

Of the 234 sightings of zebra during radio tracking sessions of roan antelope during 1996, 165 were in the vicinity of waterpoints. Of the 146 sightings of zebra grazing 85.8 % were grazing in the more open, low-lying areas rather than on the denser crests (13.2 % of encounters). Radio-tracked roan antelope were an average of 2.19 km from water (55 sightings), also showing a significant selection for grazing in the low-lying areas (p < 0.0001) (Table 5).

Table 7

Vegetation parameters in the closed and open area of the NBP compared to the Mooiplaas basalts

Geographical zone	Biomass kg/ha	% decreasers	% increasers
Closed	5261	34	69
Open	4777	31	64
Mooiplaas basalts	5531	22	75

Vegetation responses

With the increase in rainfall after 1993 there was a general increase in biomass and in percentage decreaser species (Fig.7). The closure of waterpoints on the NBP was associated with a significantly higher biomass and percentage of palatable, decreaser species on the NBP than the other areas north of the Olifants River (Table 6). The biomass, however, did not differ significantly (p = 0.22) between the closed and open areas and the adjacent Mooiplaas basalts. The percentage decreasers were significantly higher in the closed area (p = 0.041) than in the Mooiplaas basalts (Table 7).

The detailed vegetation studies on the effect of closure of waterpoints indicated that the area around closed waterpoints changed from annual to perennial grasslands. These areas had a high abundance of palatable, perennial, decreaser species. The grassland around open waterpoints was still dominated by annuals, of which most were unpalatable increaser species (Jacoby 1999). Decreaser species such as *Themeda triandra* and *Digitaria eriantha* were also present at closed, and not open, waterpoints (Davidson 1996).

Table 8

Tuft and grazing height of grass species selected by roan from available species in 1996

Grass species	Average leaf height cm	Average grazing height cm	% of available tufts	% of selected tufts
Cenchrus ciliaris	71.3	54.6	9.63	21.99
Themeda triandra	73.9	53.2	5.96	21.23
Panicum coloratum	77.2	32.6	41.06	20.46
Panicum maximum	88.3	42.9	2.52	16.11
Eragrostis superba	55.8	40.5	2.29	6.65
Urochloa mosambicensis	53.4	14.4	9.63	5.12
Heteropogon contortus	49.8	30.4	2.75	4.86
Setaria incrassata	79.2	31	1.15	1.53
Schmidtia poppophoroides	34	34.8	12.39	1.02
Enneapogon cenchroides	25.4	10.5	3.67	0.51
Digitaria eriantha	56.7	25	1.38	0.26

The number of mopane trees, with branches broken by elephant *Loxodonta africana*, decreased with increasing distance from open waterpoints, to a level of damage that was the same as around closed waterpoints at 1600 m. Other species that were browsed by elephant around waterpoints, such as *Dichrostachys cinerea*, *Lonchocarpus capassa*, and *Combretum imberbe* were utilised up to 100 m, 200 m and 800 m, respectively, from the waterpoints (Fruhauf 1997) .

The roan antelope selected different grass species during the 1996 study, compared to the species selected in 1976 (Joubert 1976). *Themeda triandra* was the most preferred species of roan antelope in 1976, even though *Panicum coloratum* was the most abundant of the selected grass species. In 1996 *Panicum coloratum* was by far the most abundant of the species that the roan antelope utilised, but *Themeda triandra* and *Cenchrus ciliaris*, that were far less abundant than during the 1976 study made up an equal proportion of their diet (Table 8). According to 480 observations of tufts utilised, roan antelope selected to feed at an average height of 41 cm, which was below the average leaf height of 69.3 cm of the decreaser species, indicating that the grass height was suitable for roan to select the preferred parts.

Change in the lion population

Results of four lion-calling censuses suggested an initial decrease in 1995 after the closure of waterpoints. Population numbers stayed more or less constant towards 2002 (Fig. 13). After the closure of waterpoints, the mean pride size on the NBP of 6.4 (n = 39) was significantly larger than the 3.54 (n = 87) recorded when the waterpoints were still open (p = 0.0006). This was associated with changes in pride composition with a larger number of subadult males (Table 9).

Table 9

Numbers of lions in different sex and age classes on the NBP before and after closure of waterpoints

	October 1993	December 1996
Adult male	33	5
Adult female	36	24
Subadult male	6	10
Subadult female	7	7
Cub	14	5

Very few incidences of predation of rare antelope were recorded on the NBP, in spite of intense observation. There was only one record of a tsessebe calf caught by lions in 1996 and an adult roan antelope cow probably caught by a lion in April 2001.

Discussion

The rainfall during the dry cycle of the 1980s and early 1990s was the lowest in recorded history in 10 out of the 22 rainfall measuring stations in the KNP, and followed on a very wet cycle in the 1970s (Zambatis & Biggs 1995).

Vegetation monitoring only started in 1989, but by using remote sensing techniques (Botha 1997) found that the area of degraded or bare veld had increased from 6 % of the northern plains area in 1985 to 40 % in 1989. During the same period the area of healthy vegetation (by his criteria) declined from 10 % in 1985, to 3 % in 1989. The vegetation monitoring after 1989 reflected the effect of the dry cycle, with the decline of palatable, decreaser species being one of the main consequences. The vegetation surveys in 1999 indicated that the percentage decreaser grass species have not increased to the same point as in 1989 and can be presumed to have been much lower than in 1985.

The changes observed in animal numbers are most likely the result of the change in rainfall. Animal biomass would have been high at the end the very wet cycle of the 1970s (Coe *et al*. 1976) when animal counts were started, with mesic species such as tsessebe, sable and roan responding favourably to the high rainfall (Pienaar 1974; Mills *et al*. 1995b). With the onset of the dry cycle, buffalo and rare antelope numbers could be expected to decline, with zebra and wildebeest increasing (Mills *et al*. 1995b). The initial drop in roan numbers was thus not unexpected as they are one of the species most sensitive to habitat changes (Smithers 1983), and to competition from other species (Wilson & Hirst 1977). The presence of artificial waterpoints would have further favoured water-dependent species such as zebra above the rare antelope species during a period of severe drought (Owen-Smith 1996). With the increase in rainfall after 1994 zebra and wildebeest numbers would again be expected to drop, as was indeed observed, with a slow rise in the numbers of the mesic species of which only the buffalo numbers showed some evidence (Fig. 5).

Smuts (1972) commented that in spite of the fact that zebra had not over-utilised the northern plains, their large numbers led to competition with the rare antelope species such as roan. He stated that zebra numbers would have to be checked especially if the eastern boundary was to be fenced. The vegetation index maps created by Botha (1997) for 1989 show that the drainage lines (and densely wooded sandveld, which is not readily utilised by zebra or roan antelope) were the only areas with readily available biomass in 1989. Observations of radio-collared roan in 1996 show that roan and zebra preferably foraged in the low-lying drainage areas. One could thus assume that both species would have been utilising these areas during the drier periods and that roan antelope as selective feeders would have been the more disadvantaged (Wilson & Hirst 1977).

The decision to close waterpoints coincided with an increase in rainfall from 1994 onwards. This increase in rainfall and the expected resultant decline in zebra numbers in the area (Mills *et al*. 1995b), resulted in an improved field layer around the windmills as well as in the general area, seen as an increase in biomass (standing crop) and palatable decreaser species in the area of closed windmills.

In spite of the improvement of the vegetation after the closure of waterpoints and the increase in rainfall, even dry season rainfall, the habitat had not recovered totally. This is reflected by the fact that even though roan were able to feed on nutritious species such as *Panicum coloratum* they were not able to select the same percentage of *Themeda triandra* as in the 1976 study (Joubert 1976). At that time this was the most preferred species, and was identified as good indicator of where to find roan.

Rather than the expected slow increase of rare antelope in response to the improvement in vegetation, roan stabilised but did not increase, while sable and tsessebe numbers declined further after the closure of waterpoints. Sable antelope that were scattered along the drainage lines on the NBP in 1993 and 1996, had all but disappeared from the NBP in 1998, while the remaining larger herds of tsessebe were more strongly associated with waterpoints. Although the general decline of tsessebe was found to be related to the decline in rainfall (Dunham & Robertson 2001), they seemed to have reacted negatively to the closure of waterpoints, showing a substantial decline from 70 on the plains in 1993 to 40 in 1998, and 20 in 2000. Eckhardt (2000 *pers. comm.*) also found evidence of a large increase in the woody vegetation cover on the basalts and granites of northern KNP over five years, which would have made the habitat less suitable for tsessebe (Garstang 1982).

Unfortunately, the response of the rare antelope to the increase in rainfall in the rest of the KNP does not lend itself to examination, as the approach to the collection of rare antelope numbers was being adapted between 1995 and 1999. In a survey during May 1999, rangers in the KNP estimated the sable population at 507, the tsessebe population at 158, and the roan population (including 33 animals in the enclosure) at 63. These numbers are all much lower than reported in 1994 and the closure of waterpoints may not be the only reason for the decline in sable and tsessebe.

One can only speculate on the effect of the boundary fence (since its erection in 1976) in further limiting movement of roan to the southern limit of their distribution. The roan numbers started dropping 10 years after the effective closure of the area as the rainfall dropped below the mean. The restricted chance for dispersal of the dambo-loving roan to other suitable habitats was first associated with a build-up of numbers during a wet period, and then with a severe drop in the roan antelope population during the drought.

Genetic links with the eastern and northern population, rather than the western population (Mathee & Robinson 1999) seem to indicate that the roan in the KNP must have had historical links with these eastern populations. This indicates likely movement between the adjacent areas of Mozambique and Zimbabwe before the presence of fences.

Even though severe losses of roan were reported during the anthrax epidemics, the protective effect of vaccination on the population is difficult to evaluate, as there had not been similar outbreaks in the area during the vaccination campaign or thereafter. It does not seem that the vaccination procedure had a negative affect on the roan antelope, as the only remaining roan herds are still on the NBP, where they were vaccinated. Densities on the NBP remained higher than in the Mooiplaas basalts where there is also suitable habitat and where they were not vaccinated.

The possible role of predation, especially on the small remaining population, cannot be ignored. In the enclosure where the roan antelope were safe from predators, the population grew from 7 to 49 in 7 years, while the free-living populations hardly increased during the same period. Roan had been reported to fall prey to lions even during the previous wet cycle, and over 22 years, rangers reported 90 roan killed by lion which formed 1.11 % of the lion diet. From these reports it was estimated that 4–12 % of adult roan fall prey to lions every year. Harrington *et al.* (1999) developed a model that explained the initial steep decline in the roan population by predation. In a subsequent study, McLoughlin (2001) found that at predation rates of 15 % the viability of the current small free-ranging population over the next 50 years is low.

Conclusion

Over the span of several decades, the equilibrium-centred "command and control" approach aimed at the conservation of elements such as species, of which the rare antelope was of specific concern, seems to have been very successful. However, the increased availability of perennial water and limitation of movement to other habitats removed important sources of variation. Thus the system may not have been able to adapt to the severe and prolonged drought, as its ability to do so had been reduced resulting in a reduction in system variation (Holling & Gunderson 2002). The new management approach involving closure of waterpoints, the opening of boundary fences as well as the readjustment of the fire management to a less controlled regime, should again increase the ecosystem resilience (Holling & Gunderson 2002). However, the time scale for this resilience to take effect is probably several decades and possible negative short-term results have to be considered carefully.

This study also illustrates the difficulties involved in conserving low numbers of a species at the limit of their distribution. The habitats of these rare antelope in the KNP may be marginalised even further, as global climate models mostly predict drier and warmer conditions in the decades ahead, with an associated increase in woody biomass (Rutherford *et al*. 1999).

In "nature evolving" management approaches emphasising ecosystem resilience, an adaptive management approach needs to be adopted (Rogers *et al*. 2000; Holling & Gunderson 2002). Parameters to indicate thresholds of potential concern (TPCs) were developed for herbivores and vegetation and were incorporated in the new KNP management plan (Braack 1997). These limits were implemented to elicit further management responses to the persistent small roan antelope population and the declining tsessebe population and led to the decision to expand the captive breeding facilities (Grant & Van der Walt 2000).

The challenge for rare antelope conservation will be to decide how to balance the need for resilient ecosystems with the specialised requirements of marginal species.

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