# Aspects of wildebeest *Connochaetes taurinus* ecology in the Etosha National Park - a synthesis for future management

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ABSTRACT

Studies of wildebeest *Connochaetes taurinus* ecology (1975-78) concluded that human activities, notably fencing off of former migration routes, eliminated the ability of wildebeest to migrate. This reduced a population, estimated at 25 000 in 1955, to 3 700 when fencing of Etosha was completed in 1973. The residual population in Etosha was subjected to elevated levels of anthrax to which most wildebeest are susceptible, but to which predator-scavenger populations of lion *Panthera leo* and spotted hyaena *Crocuta crocuta* in Etosha have developed immunity. Additionally, artificial water points further stabilised the environment for these carnivores, contributing to a decline in wildebeest numbers to 2 500 by 1978 and 2 170 in 1993. Moreover, nutrition, especially crude protein and inorganic phosphorus, may seasonally be below maintenance levels of large, grazing herbivores in Etosha. These studies took place during a phase of above-average rainfall in which the supply of nutrients was liberal. The danger of a critical nutrient deficiency in large herbivores, especially wildebeest, seems likely during a prolonged drought. Since 1978 wildebeest numbers have fluctuated between 2 200 and 2 600. Future options available for corrective management of the wildebeest population in Etosha are provided.

## INTRODUCTION

A study of wildebeest in Etosha was done from 1975-78 (Berry 1980) and this is primarily a synopsis of that work. To avoid the inclusion of numerous references in the text, the unpublished thesis of Berry (1980) serves as a source for literature prior to 1980, however, key references prior to 1980, which relate to work outside Namibia plus constraints and conclusions, are provided. Furthermore, details of the various aspects of wildebeest ecology studied have appeared in a series of publications which are referred to under each subject heading. I first present a brief review of the history of wildebeest in the Etosha region, followed by the findings of the 1975-78 study, including the predictions which were made. Relevant data collected on wildebeest since 1979 are incorporated. Using this knowledge, various options for adaptive management, which may ensure a viable population of wildebeest in the Etosha National Park, are identified.

## HISTORY OF WILDEBEEST IN NAMIBIA

Wildebeest featured prominently for the first time in Namibia's recorded history in 1896 when German troops stationed at Namutoni, Okaukuejo and Sesfontein were given orders to shoot migrating game to curb the spread of rinderpest virus (Fischer 1914). When commercial farming began in the areas east and south of Etosha during the early half of this century, wildebeest were shot on an ongoing basis by farmers who feared for the transmission of malignant catarrhal fever and blue wildebeest eye (Afrikaans "uitpeuloog") to their cattle (Gaerdes 1977).

Estimates of wildebeest numbers prior to aerial censuses in 1968 must necessarily be regarded as subjective and, in some cases, as little more than enlightened guesses. The first estimate of wildebeest numbers which could be traced for South West Africa (SWA, now Namibia) was by Fischer (1914) when a figure of 8 000 was given for the Kalahari districts of eastern SWA. An additional 5 190 wildebeest were said to exist in the adjacent Kalahari of Botswana (Fischer 1912 in Gaerdes 1977). However, it was said that wildebeest were "the most plentiful of large open-country antelope in SWA" during the early 20th century (Shortridge 1934). Jaeger (1926-27) wrote that 20 000 to 30 000 wildebeest occurred on the plains of Etosha in 1913. In 1926, when the first status assessment of wildlife in the entire SWA was undertaken, figures were available for 15 magisterial districts of which 6 reported the presence of wildebeest: Gobabis (3 200), Gibeon (2 000), Aroab (600), Otjiwarongo (300), Okahandja (17) and Grootfontein ("fairly numerous"). Therefore in 1926 at least 6 117 wildebeest were estimated to be present on commercial farms and 17 500 in the Etosha-Owambo area (Figure 1), giving a total of 23 617 in SWA. Other estimates were made prior to aerial censuses, for example 7 000 to 10 000 in 1952 (Schoeman 1952), 25 000 in 1954 (de la Bat, pers. comm. 1977) and 30 000 in 1965 (Viljoen 1967).

The next wildlife survey for SWA was done in 1975 (Joubert & Mostert 1975). It produced an estimate for wildebeest of 245 on commercial farms, 500 on tribal land and 3 717 at Etosha (Figure 1); a total of 4 462.

The historical distribution of wildebeest in Namibia, based on recent evidence (Lindeque in press), was as far south as the Orange River and east of the Fish River. This is greater than the area described by Shortridge (1934). The range has subsequently been reduced to the central and eastern sections of Etosha, where probably the only viable population of free-living wildebeest in Namibia remains. As elsewhere in Africa the decline in wildebeest numbers began with the Pan African rinderpest epidemic at the end of the 19th century, gaining momentum when veterinary controls such as large-scale shooting of wildlife took place and cordon fences were erected. International boundary fences, game reserve fences, farm fences, and illegal hunting of wildebeest on State and communal land, further contributed to the decline in SWA. Thus all

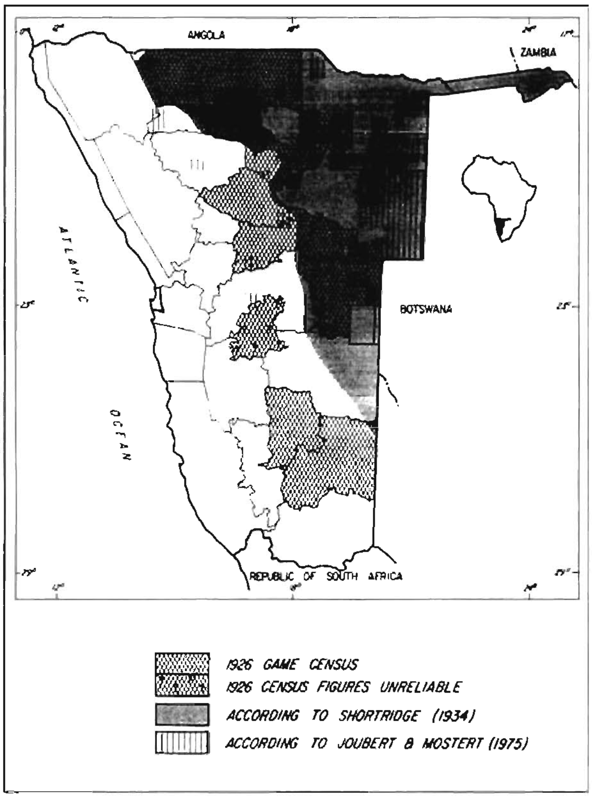


FIGURE 1: Past and present distribution of blue wildebeest in Namibia (1926, 1934, 1975).

accounts indicate that, prior to restrictive fencing, wildebeest occurred throughout eastern and north-eastern SWA, probably migrating in an unrestrained manner to neighbouring Angola and Botswana (Sidney 1965). The probability of a linkage to the East African populations via a "drought corridor" (Bigalke 1972) is shown in Figure 2. Investigations carried out subsequent to my study emphasize the value of migration to wildebeest survival (Fryxell, Greever & Sinclair 1988; Williamson, Williamson & Ngwamotsoko 1988; Whyte & Joubert 1988; Spinage & Matlhare 1992).

The first aerial census of Etosha took place in 1968 and estimates became more refined as census techniques improved (Table 1). From these it was apparent that the wildebeest population was in a state of decline, being 3 300 when the study commenced. Therefore the primary aim of this investigation was to establish which of the major environmental factors such as climate, food, water, disease and predation may have become limiting to Etosha's wildebeest and then make recommendations for management practices to halt and possibly reverse this decline.

## CLIMATE (Berry, Siegfried & Crowe 1984)

It was not expected that Etosha's climate would prove limiting to wildebeest, however for the sake of completeness it can be stated that they responded predictably to the ambient sun and wind regimes, presenting the long axis of their body to the sun when temperatures were low to facilitate heat uptake. Conversely, when temperature increased above 22°C they orientated their body axis parallel to the incoming radiation, thereby compensating for excessive heat load. Shade was used when available to provide additional relief from direct solar radiation. At wind speeds greater than 12 km/h wildebeest faced into the airflow, often maintaining this position while they moved to drink (thereby facilitating their awareness of possible predators lying in ambush). When the sun's altitude increased to 85° during the summer solstice, body orientation became random between 4 and 8 hours after sunrise because it had little bearing on the sun's overhead position. It was consequently concluded that sun direction is probably of greatest importance to body orientation in wildebeest in early morning and late afternoon, while wind may impinge on this reaction, influencing the body position during the midday heat and when wildebeest move to a watering point.

In a similar study in South Africa, Ben-Shahar & Fairall (1987) concluded that shading, especially in summer, was a significant thermoregulatory adaptation in blue wildebeest. However, while orientation of the body is related to sun and wind in Etosha's wildebeest, it is not the case where sufficient shade is available (Shahar & Fairall 1987).

During the study period (1975-78) a total of 26 major (at least 10 $km^2$) natural fires, started by lightning, occurred in Etosha. In the same period 13 artificially induced, major fires occurred (Siegfried 1981). During the 9-year period 1970-79, a wet phase in Etosha, the number of major fires on the plains where most wildebeest occur was nil to 1, compared to 2 to 5 major fires in the adjoining woodlands during the same period (Siegfried 1981). This frequency indicates that the effect of fire on wildebeest

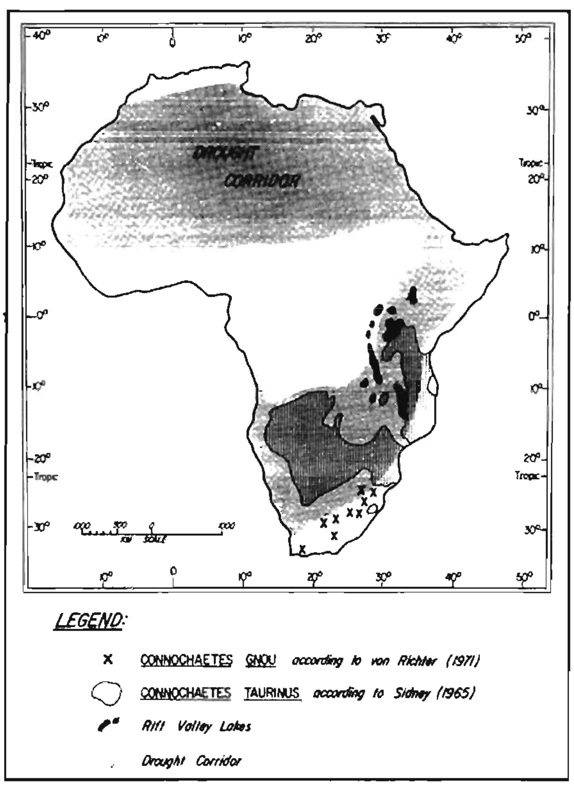


FIGURE 2: Distribution of wildebeest in Africa. The shaded area represents the "drought corridor".

habitat is minimal even during wet climatic phases, and likely to be insignificant in a dry climatic phase.

Table 1. Total and sample counts of wildebeest at the Etosha National Park, Namibia (1968-93). All censuses were total counts except in 1990 when a sample count was done.

| Year | Month | | Aircraft | Number of of wildebeest | 95 % confidence limits |
|---|---|---|---|---|---|
| 1968 | Sept. | FW | (Piper Cub) | 4 073 | |
| 1969 | April | FW | (Piper Cub) | 4 773 | |
| 1970 | Feb. | FW | (Piper Cub) | 4 789 | |
| 1972 | Oct. | FW | (Piper Cub) | 3 078 | |
| 1973 | Sept. | H | (Bell 47) | 3 717 | |
| 1974 | July | H | (Hughes 300C) | 3 300 | |
| 1976 | May | FW | (Piper Cub) | 2 360 | |
| 1976 | July | H | (Hughes 300C) | 2 638 | |
| 1976 | Dec | FW | (Piper Cub) | 2 659 | |
| 1977 | March | H | (Hughes 300C) | 2 636 | |
| 1977 | Sept. | FW | (Piper Cub) | 2 688 | |
| 1978 | March | H | (Hughes 300C) | 2 493 | |
| 1982 | May | FW | (Cessna 210) plus | | |
| | | H | (Bell 47) | 2 195 | |
| 1984 | Sept. | FW | (Cessna 210) plus | | |
| | | H | (Bell 47) | 2 253 | |
| 1987 # | Sept. | FW | (Maule Lunar) plus | | |
| | | H | (Bell Jet Ranger) | 2 617 | |
| 1990 # | Aug. | FW | (Maule Lunar) | 2 512 | 1 437 - 3 587 |
| 1993 * | Mar. | FW | (Cessna 182) | 2 170 | |

# Lindeque & Lindeque (1987, 1997). * Gasaway & Gasaway (1994). H = helicopter, FW = fixed-wing

## ACTIVITY PATTERNS (Berry, Siegfried & Crowe 1982)

By using marked individuals as focal animals (263 hours) and scanning herds (2 515 diurnal scans, 490 nocturnal scans) over a period of 1 year, it was established that the wildebeest population at Etosha spent about 53 % of its total time resting. Approximately 33 % was devoted to grazing and 12 % to movement which included walking, trotting and galloping. Overt social encounters occupied 1,5 % of the species' time while drinking water and suckling took up less than 0,5 % of total time.

Furthermore, mixed herds grazed less and moved more than bull (bachelor) herds. Mixed herds also rested more and this may have been a result of them occupying better grazing areas which reduced foraging time. However, mixed herds were obliged to move greater distances to drink because the better grazing was further from permanent water. Increased resting and a decrease in grazing time during summer was also observed in wildebeest in South Africa (Ben-Shahar and Fairall 1987).

The 24-hour cycle of activity in wildebeest was influenced by several environmental cues: primarily photoperiod which was crucial in determining the dawn and dusk activity peaks. Increasing temperature appeared to be responsible for the diurnal period of inactivity. This combination of proximate factors determined the basic activity pattern with other extrinsic influences, such as predators, modifying it. The synchrony within wildebeest herds was nevertheless always apparent and could be demonstrated quantitatively within a 24-hour cycle.

## ENERGY AND PROTEIN BUDGETS (Berry & Louw 1982a)

To determine whether there was sufficient production of these 2 critical components by the grasslands for wildebeest, on a yearly and seasonal basis, an energy budget for wildebeest was constructed by translating their activity patterns into theoretical requirement values. This enabled calculation of the energy required for maintenance and activity while allowing for energy expenditure for growth, gestation, lactation and homeothermy. A protein budget for free-ranging wildebeest was approximated for the basic life processes of maintenance, growth, gestation and lactation, using values calculated for wild and domestic ungulates elsewhere. Allowance was made for the differences between the requirements of five major age-sex and social classes of wildebeest, and seasonal changes occurring in their population structure.

Mean increments over resting metabolic rate (RMR) for wildebeest were found to be 1,30 for maintenance and activity, 0,66 for growth, 0,07 for gestation, 0,33 for lactation, and 0,22 for homeothermy. Calves had the highest energy coefficient (2,31 RMR), immature and sub-adult bulls and cows were marginally lower (2,15 and 2,04 RMR respectively), reproductive cows had an energy coefficient of 1,91 RMR, with the lowest coefficients found in adult bulls (1,56 RMR) and non-pregnant/dry cows (1,51 RMR).

When this was extrapolated for the relative contribution of each major age-sex and social class in the population, the mean increment was 1,94 RMR. Since not all aspects of energy expenditure were investigated, an increment of 2,0 RMR was considered to be a realistic energy coefficient for free existence in Etosha's wildebeest. Thus the yearly population energy budget of the 2 500 wildebeest estimated to be present at the end of the study (1978) was calculated at 21,3 terajoules which was equal to 8,5 gigajoules for an individual wildebeest. Due to the high energy content of wildebeest milk, the precocity of calves and their swift growth, it is obvious that growing animals and reproductive cows are the most vulnerable to nutritional stress. These data are similar to other wild ungulates studied in North America.

To approximate a protein budget, the wildebeest population was divided into 10 major age-sex and social classes, the numbers and biomass of which were determined on a seasonal basis. Nitrogen requirements were subsequently converted to a protein budget. Similar to their energy budget, it was evident that reproductive cows and their calves had the highest protein requirement throughout the year (199 g/day per cow, 76 g/day per calf) as well as seasonally (65 % of the population's total protein intake). This was 2,2 times the requirement in bulls and 2,9 times the requirement in non-reproductive cows. To meet the demands of free existence, the 2 500 wildebeest at Etosha would require 106 280 kg protein a year, failing which the reproductive cows and their calves would be the most vulnerable. This must be considered a first approximation because of the assumptions made necessary by the absence of nutritional data for wild African ungulates. It is, however, the first quantified investigation into the protein budget of wildebeest in an unrestrained state.

## NUTRITIONAL MEASUREMENTS (Berry & Louw 1982b)

Having established approximate requirements of energy and protein in wildebeest, it was necessary to determine quantitatively whether sufficient food and water were available to them and what the quality was on a seasonal basis. To refine this equation of requirement and supply, the food intake and faecal production of wildebeest was included in the model.

Grass samples from 7 major wildebeest habitats were sampled by hand for chemical analysis at 3 stages of growth: sprouting and seeding (January through April) and at dormancy (August). Although hand-sampling introduced a bias, it was not possible to obtain fresh grass samples of the selective feeding done by wildebeest. Proximate analyses, using standard AOAC (1965) methods, of the effects of area, season and growth stage of grass foraged by wildebeest were done. The results showed a high mean level of protein (17,7 %) during the sprouting stage, decreasing to 10,7 % at seeding and 4,1 % at dormancy. This reduction was reflected by a concomitant increase in the amounts of soluble carbohydrates and crude fibre. The moisture content of sprouting grass also declined from 74 % to 58 % (seeding) and 5 % (dormancy), corresponding with the highly seasonal rainfall at Etosha and the reduced availability of drinking water. Average metabolisable energy (ME) value in grass samples was 11,49 MJ/kg.

Rumen samples from 8 wildebeest shot for veterinary investigation in the wet season (March), and 8 similarly taken in the dry season (November), showed that 96,5 % of wildebeest diet consisted of grass. Furthermore, protein-rich grass leaf and sheath were selected (75,4 %) during the wet season. In the dry season, reduced availability of grass leaf compelled wildebeest to feed on less nutritious grass stems which then comprised 61,5% of their diet, compared to only 14,1 % in the wet season. Dry matter (DM) food intake by the wildebeest population, which was estimated at 2 269 individuals in mid-1978, was calculated to be 3 617 tons DM forage annually, or 1,58 tons DM forage annually per wildebeest. When an arbitrary minimum requirement level for wildebeest of 5 - 7 % crude protein was applied to the seasonal situation at Etosha, it was evident that a surplus of this critical nutrient was available during four months of the year (January through April). Although the dry season dormancy level of grass crude protein declined to less than the arbitrary minimum, the ability of wildebeest to synthesize protein via microbial action in the rumen and by recycling of urea in the saliva, probably compensated partly for this shortfall. Nevertheless, because Etosha's wildebeest are subjected to nutritional stress during the dry season, a shortfall in crude protein may become a critical factor for limiting the population, especially during prolonged droughts. There was, however, no shortfall of highly digestible energy in the grass available to wildebeest throughout the year. Also, no significant seasonal relationship between the quality of grass and the crude protein and fibre composition of freshly collected wildebeest faeces could be established.

Kidney efficiency in wildebeest was rated by relating medulla thickness to kidney size. The maximum plasma : urine osmotic ratio was 1 : 5,7; therefore wildebeest appeared unable to reduce water loss significantly via their urine. Also, faecal water loss remained high throughout the year. Water sample analyses of the major natural and artificial sources gave higher dry season bacterial counts and natural springs had a higher incidence of bacteria than bore-holes. Similarly, spring water contained more chemicals and was more alkaline than bore-hole water. Wildebeest favoured natural springs during the dry season and drank exclusively from rain-water pools in the wet season.

At Etosha, as in other areas of Africa, wildebeest appeared to be dependent on water, preferring to drink daily during 94 % of the observations. They rarely went without drinking for more than 2 days. Moreover, all wildebeest were recorded within a radius of 15 km from drinking water during the dry season, when the majority (72 %) were less than 10 km from water. Their water dependency may have imposed restrictions on their foraging ability at a time of year when the quality of grazing was at its poorest. Wildebeest milk was a source of high energy for the precocious calf, greatly exceeding that of a dairy cow (6,14 J/g compared to 2,91 J/g), but consistent with other tropical Artiodactyla. The levels of fat, protein and lactose in wildebeest milk aided rapid growth in calves, estimated to average 230 g increase daily for the first year. Increased nutrients in wildebeest milk resulted in a corresponding reduction in its water content to 78 %, thereby favourably reducing the nursing cow's water requirements.

When the quality of forage, its moisture content, and the availability of drinking water were considered, it was apparent that Etosha's wildebeest existed under ideal conditions for about 4 months of the year (the wet season from January through April). The surplus of grass on the plains available to wildebeest and their major food competitors, namely Burchell's zebra, gemsbok, springbok, red hartebeest and ostrich, during the wet season was evident when the measured energy balance was found to be 1,2 times greater than the measured usage. Similarly, the measured crude protein balance exceeded the measured usage by 2,5 times. Due to the critical food-water link in wildebeest, they experienced increasing difficulty in obtaining good quality food for the remaining dry season of 8 months. Nevertheless, in the years of average and above average rainfall which were experienced during the study, the population did not appear to be limited by nutrition. However, it was predicted that during dry climatic phases nutrition, especially protein deficiency in the 8-month dry season, may prove limiting to Etosha's wildebeest.

## SEASONAL NUTRITIVE STATUS (Berry & Louw 1982c)

To assess objectively the nutritional status (or "condition") of free-ranging wildebeest, internal examinations were used in conjunction with subjective assessments of the external physical appearance of a large and representative sample of the population at critical seasons. Thereby the visual physical rating of a sample of 3 898 wildebeest showed 14 % to be in excellent condition, 64 % in good condition, 21 % in fair condition and less than 1 % in poor to very poor condition. At no stage of the 3-year visual sampling period did the population appear to be physically stressed. This was supported by the kidney fat index and by bone marrow sampling when 8 out of 10 wildebeest had a marrow fat level of more than 88 % in the wet season (March) and 6 out of 10 had more than 78 % marrow fat in the dry season (November). Lowered levels of marrow fat were associated with rutting, pregnancy, lactation and, in the case of calves, separation from the mother.

Analysis of 9 blood parameters and liver analysis confirmed nutritional level to be normal except for inorganic phosphorus which remained below the acceptable level for bovines throughout the year. Osteophagia, which may be a primary clinical symptom of phosphorus deficiency in the diet, was however not recorded in wildebeest. Other symptoms of a phosphorus deficiency, such as osteoporosis, lowered fecundity and elevated mortality rates, could not be directly measured in the free-living population. Therefore, although phosphorus may be only marginally deficient, its chronic shortage in Etosha could contribute to a decline in the population. Levels of copper and cobalt in the blood and liver may also have been marginally deficient but this too was not manifested by clinical evidence. Also, gross haemocytological investigation revealed no cellular abnormalities, supporting the findings that trace element supply was adequate. The overall conclusions reached were that the nutritive status of wildebeest at Etosha was sufficiently high to discount nutrition as a factor limiting the population during the study, a period of above-average rainfall, when the supply of nutrients was liberal.

## DISEASE AS A LIMITING FACTOR (Berry 1981a)

To establish the role of disease, a total of 127 wildebeest carcases and 337 carcases of other large herbivores such as Burchell's zebra, gemsbok, springbok, red hartebeest, and ostrich were monitored over a 3-year period (1976-78). In the same period 60 immobilised wildebeest were visually examined for external parasites and peripheral blood smears were scanned for blood parasites. In addition, 25 wildebeest were selectively sampled by veterinarians for detailed pathological and parasitological investigations. The endoparasite profile was low, while the ectoparasite burden was exceptionally low, except for *Gedoelstia* larval counts which approached typical herbivore levels.

Anthrax, caused by the bacterium *Bacillus anthracis* was identified in 62 % of wildebeest carcases, 43 % of zebra carcases, 21 % of springbok carcases, 10 % of gemsbok carcases, and absent in hartebeest and ostrich carcases. Mortalities from anthrax peaked during the rainy season when the bacillus was identified in blood smears from carcases of wildebeest (76 %), zebra (51 %), and springbok (40 %). There was no significant sex link in wildebeest mortality due to anthrax but the death of reproductive cows resulted in the loss of unweaned calves.

Ebedes (1976), suggested that environmental conditions at Etosha, especially the alkaline nature of the soil and water, coupled with poor drainage, favoured anthrax viability. Prior to 1964 mortality in wildlife was not recorded regularly, however de la Bat (pers. comm. 1977), Rochèr (pers. comm. 1977) and Stark (pers. comm. 1974) were not aware of anthrax outbreaks before that date. This may indicate that prior to 1964, when wildebeest in SWA were said to number 25 000, anthrax was a minor cause of mortality in herbivores at Etosha.

Taking into account the findings that neither food nor water were limiting for the wildebeest population and the fact that their nutritive status was good, it appeared evident during this study that disease in the form of anthrax was a major factor in the reduction of the wildebeest (and the zebra population) remaining in Etosha following its complete fencing in 1973.

In the 30-year period that mortalities were recorded in Etosha (1964-94: Table 2), the first 15-year period (1964-79) was characterised by a higher incidence of anthrax in plains dwelling grazers such as zebra, wildebeest and springbok, when 1 513 carcases of these 3 species were confirmed or suspected to have died of anthrax (Lindeque 1991). This higher incidence partly coincided with a wet phase which began in 1967 and continued until 1978. It was followed by a dry phase which has persisted until 1996. During the second 15-year period of mortality records, the incidence of anthrax in zebra, wildebeest and springbok declined (928 carcases confirmed or suspected anthrax), whilst anthrax in elephants was responsible for 31 % of all confirmed and suspected cases in wildlife (Lindeque 1991). Anthrax is currently regarded as being the major factor limiting Etosha's elephant population, but no longer to be limiting to wildebeest or zebra populations (Lindeque 1991).

TABLE 2: Confirmed and suspected cases of wildebeest killed by anthrax, compared to other large herbivores and carnivores in the Etosha National Park (1964-94). n = 3 046 records. Sources of data: Ebedes (1970, 1974, 1976); Lindeque (1991), mortality records at Etosha Ecological Institute, Okaukuejo.

| SPECIES (percentage in brackets) | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| CT | EB | LA | AM | OG | TS | GC | DB | TO | EZ | SC | AJ | RC | AB |
| 832 | 1365 | 487 | 244 | 37 | 24 | 18 | 13 | 6 | 6 | 6 | 5 | 2 | 1 |
| (27) | (45) | (16) | (8) | (1,2) | (,8) | (,6) | (,4) | (,2) | (,2) | (,2) | (,2) | (,1) | (<,1) |

CT = wildebeest *Connochaetes taurinus*, EB = Burchell's zebra *Equus burchellii*, LA = elephant *Loxodonta africana*, AM = springbok *Antidorcas marsupialis*, OG = gemsbok *Oryx gazella*, TS = kudu *Tragelaphus strepsiceros*, GC = giraffe *Giraffa camelopardalis*, DB = black rhinoceros *Diceros bicornis*, TO = eland *Taurotragus oryx*, EZ = Hartmann's zebra *Equus zebra hartmannae*, SC = ostrich *Struthio camelus*, AJ = cheetah *Acinonyx jubatus*, RC = steenbok *Raphicerus campestris*, AB = red hartebeest *Alcelaphus buselaphus*

## PREDATION AS A LIMITING FACTOR (Berry 1981a)

While predation and scavenging are normal and desirable for the maintenance of healthy herbivore populations, most terrestrial systems, including Etosha, have been influenced by modern human activities. This may have resulted in abnormal predator-prey ratios as evidenced elsewhere in Africa (Pienaar 1969; Schaller 1972; Smuts 1975-76, 1978a, b, c, 1982). Consequently, the numbers, age-sex ratios, group size, prey preferences and food intake of large carnivores at Etosha were estimated. These data were used to establish whether the predator-prey ratio was within acceptable limits when compared to other African conservation areas.

At Etosha, a portion of carnivores' food is provided by animals which die of anthrax. Thus, during an anthrax outbreak, lion and spotted hyaena need not hunt with normal frequency, but can scavenge from anthrax-infected carcases. Moreover, these carnivores have acquired an immunity to anthrax (Lindeque 1991), facilitating their survival and increase in numbers.

Based on a mean daily food intake by large carnivores of 5 % of body mass, it was estimated that 21-30 % of the large herbivore biomass (1 000 - 1 500 tonnes) was removed annually from the plains of Etosha by predating or scavenging lion and spotted hyaena, plus predating cheetah. Taking the minimum figure of 21 % removal, it was evident that neither wildebeest nor zebra, which together comprised 80 % of lions' recorded diet and 62 % of the recorded cases of anthrax, could withstand these combined mortality pressures. This was confirmed by the substantially lower recruitment rates of these herbivores to the breeding stock (11 - 18 % for wildebeest, approximately 8 % for zebra). It is therefore not surprising that the wildebeest population decreased by 24 % (from 3 300 to 2 500) during the study, while zebra numbers declined by 43 % (16 000 to 9 000) during the same period. Etosha's predator-prey ratios were estimated at 1 : 107 - 153 (minimum and maximum) for lion and 1 : 72 - 105 for lion, cheetah and spotted hyaena numbers combined. These ratios were considerably higher than in most other African conservation areas and similar to Kruger National Park, South Africa (1 : 57 - 149) where lions were considered so numerous that 335 were culled in a period of about 3 years (Smuts 1982).

The conclusion reached was that at Etosha the large carnivore populations had become relatively sedentary and increased in abundance due to the provision of artificial drinking places, including gravel pits for road construction, plus the seasonal abundance of food in the form of anthrax carcases. In the latter situation more anthrax-infected carcases were available during localised epizoötics than what scavengers were able to dispose of. In the absence of practical control measures for anthrax at Etosha during epizoötics, recommendations were made to indirectly control lions and spotted hyaenas by closing a number of artificial water-holes, in preference to culling. Later, long-acting hormone contraception was tested on adult lionesses and found to be a practical and effective birth control mechanism for the species (Orford, Perrin & Berry 1988).

## POPULATION SIZE, STRUCTURE, MORTALITY PATTERNS, AND A PREDICTIVE MODEL (Berry 1981b)

The earlier estimates of between 10 000 and 30 000 wildebeest have been questioned by some researchers who maintain they were too high. These estimates origi-

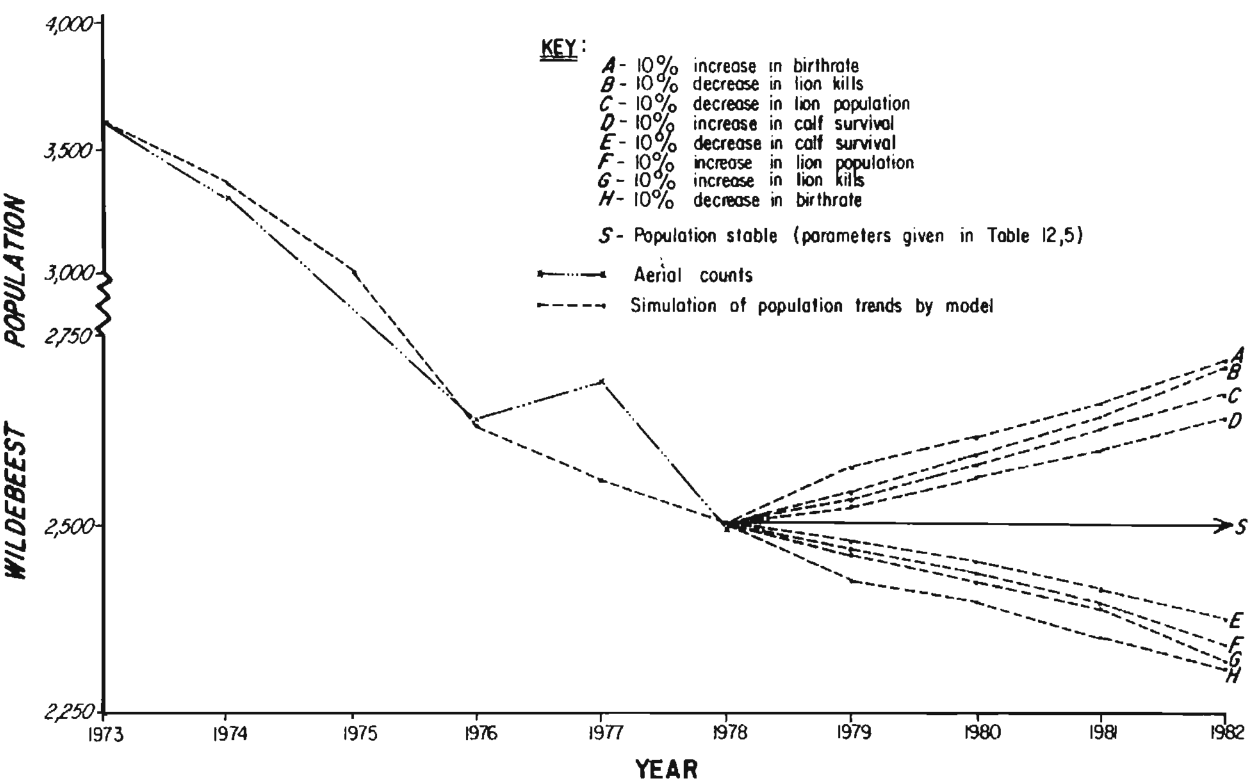


FIGURE 3: Wildebeest population model and predictions for future trends at Etosha (1973-82).

nate from early explorers, the first biologists of Etosha, veterinarians and agricultural officers who worked in the area (SWA File A.201/10 1926; Jaeger 1926-27; Schoeman 1952; Viljoen 1967; de la Bat 1977 pers. comm.). Even if the accuracy of these estimates is debatable, as with all historical estimates of abundance, the important issue is that, prior to farm fences in the 1950s, veterinary cordons in 1961, and Etosha's fencing in 1973, wildebeest migrated in an unrestrained state throughout most of northern and eastern SWA. Furthermore, the apparent order of magnitude of decline accompanying restrictive fences is sufficient evidence to accept that fencing prevented the species from using traditional migration routes. The record of wildebeest succumbing elsewhere in Africa to drought-related conditions when fencing curtails their traditional migration routes supports the conclusion that wildebeest populations will decline if denied the ability to migrate (Campbell 1981; Owens & Owens 1984, Whyte & Joubert 1988; Williamson, Williamson & Ngwamotsoko (1988).

Wildebeest excluded from Etosha when it was totally fenced in 1973 were probably mostly eliminated by hunting. Those remaining within Etosha's boundary decreased from 3 717 to 2 493 between 1973-78, a reduction of 33 %.

Having established the major causes of the reported sharp decline in wildebeest numbers in SWA to be fences which prevented migration, disease in Etosha which periodically reached epidemic proportions, and artificial water points in Etosha which stabilised the environment for carnivores, it was necessary to examine the effects of these agents on the wildebeest population size and its structure. To achieve this the results of aerial and ground censuses, observations for age-sex ratios, and age determination of carcases were employed. Using these data it then became possible to develop a predictive model, based on that of Starfield, Smuts & Shiell (1976), by changing critical parameters such as number of lions, yearly kill rate of lions, calf survival rate and birth rate (Figure 3).

Calf survival rate was taken at 0,5 on average, simulating the mortality from the end of the calving period to 1 year of age (Talbot & Talbot 1963). To simulate adult birth rate the percentage of adult cows (63 %) in the Etosha population was multiplied by the pregnancy rate, estimated by observation to be 87 %. Consequently, the upper limit for birth rate in Etosha would be 0,54. However, to reflect losses from aborted pregnancies, still-born calves and neonate deaths, a lower value of 0,35 was used. In determining this figure, account was taken of the fact that up to 50 % of neonates may die (Talbot and Talbot 1963). By comparison, precocious 2-year old wildebeest cows in Kruger National Park had a birth rate estimated at only 0,21 (Starfield *et al.* 1976). Thus, plausible mean values of 0,35 for birth rate and 0,5 for calf survival, in conjunction with varying predation rates for wildebeest older than 1 year, were used in a computer model to project changes in the population for 10 years (1973-82).

The population structure of Etosha's wildebeest was compared to a population in Zululand, South Africa (Table 3) which was estimated to be declining at approximately 4 % annually (Attwell 1977). Calf percentage in Etosha was higher, but single, territorial bulls were proportionately fewer than in Zululand. This disparity was compensated for by the relatively larger bachelor herds at Etosha. Maturing wildebeest showed a disproportionate, male-biased mortality, resulting in an adult sex ratio of 1 bull : 1,57 cows which closely resembled the adult sex ratio of 1 : 1,49 in the Zululand wildebeest population.

TABLE 3: Population structure of Etosha's wildebeest (1976-78) compared to a Zululand wildebeest population investigated by Attwell (1977).

| CRITERIA USED | AREA ETOSHA* | AREA ZULULAND** |
|---|---|---|
| No. of wildebeest sampled | 3 907 | 800 |
| Sample as % of population | 31,0 | 30,0 |
| % Single, territorial bulls | 3,7 | 9,0 |
| % Breeding herd bulls | 2,7 | 5,5 |
| % Bachelor herd bulls | 14,9 | 11,9 |
| Mean size of bachelor herds | 8,4 | 5,6 |
| Range in size of bachelor herds | 2 - 120 | 2 - 16 |
| Total % of full-grown bulls | 21,0 | 26,4 |
| Total % of breeding herds | 79,0 | 79,1 |
| Mean size of breeding herds | 33,7 | 14,4 |
| Range in size of breeding herds | 2 - 370 | 2 - 40 |
| % Calves in breeding herds | 39,0 | 19,4 |
| % Calves in total population | 22,0 | 15,4 |
| No. of calves per 100 adult cows | 67 | 40 |
| % Immatures (1 - 2 years) | 14,0 | 19,8 |
| % Sub-adults (2 - 3 years) | 10,0 | - |
| % Adult cows | 33,0 | 38,5 |
| Immature bulls : immature cows | 1 : 1,17 | - |
| Sub-adult bulls : sub - adult cows | 1 : 1,53 | - |
| Adult bulls : adult cows | 1 : 1,57 | 1 : 1,49 |
| Calves : adult cows | 1 : 1,50 | 1 : 2,50 |

* Based on ground observations (1976-78)
** Based on aerial observation (August 1974)

Mortality patterns in young wildebeest could not be established accurately because skulls of calves and immatures were frequently destroyed by carnivores. Based on tooth eruption and attrition, a sample of 283 skulls revealed that adult mortality in both sexes was greatest between 3 and 6 years of age (48 % of all skulls found). By 10 years of age 91 % of adults had died. Maximum longevity recorded was approximately 14 years. Etosha wildebeest died at a younger age than in other areas of Africa and did not match the longevity of up to 21 years recorded elsewhere. This may be due to the incidence of anthrax and a high level of predation in prime age wildebeest. Lion "kills" were assumed to be the ultimate factor in wildebeest mortality above the age of 1 year, although anthrax was in many instances the proximate factor. Birth rate was found to be the population parameter most sensitive to change, followed by lion kill rate, the number of lions, and lastly, calf survival rate. The model was a gross simplification of the complicated ecological processes governing the wildebeest population. It nevertheless illustrated the fact that the former numbers of wildebeest (prior to fencing of Etosha) are unlikely to be regained.

If the predictive model in Figure 3 is compared with the total aerial censuses in 1982 and 1984 when 2 195 and 2 253 wildebeest were counted respectively (Table 1), it shows a decline exceeding the projected 10 % for the 4 major parameters used. In 1987 and 1990 the wildebeest population showed an increase to 2 617 and 2 512 respectively (Table 1), but in March 1993 a total of 2 170, the lowest number of wildebeest yet recorded in Etosha, was the total estimated population. This low figure was ascribed to unusually high calf mortality in 1993 Gasaway & Gasaway (1994).

## SUMMARY OF ABIOTIC FACTORS LIMITING WILDEBEEST (1956 TO 1994)

In an investigation of the mosaic-cycle concept of ecosystems (Aubreville 1938; Remmert 1991) as applied to natural events in arid and semi-arid Namibia, rainfall at Etosha was identified as the primary agent driving the system (Berry & Siegfried 1991). Successive wet and dry phases of 10-16 years have been recorded in Etosha, yet despite years of above average rainfall and good production of grass, wildebeest (and zebra) numbers have suffered spectacular decreases. Rainfall at Okaukuejo has been recorded since 1956 and is highly variable: the long term mean (n = 38 years) is 347,4 mm (median = 332,8 mm), but the range is several orders of magnitude (minimum = 194,8 mm, maximum = 677,8 mm). Despite the clearly apparent wet and dry periods, no statistical correlation between amounts of rainfall and any of Etosha's large mammals, including wildebeest, was found (Berry & Siegfried 1991). While rainfall is a primary agent in Etosha, the influence of human activities, such as game-proof fencing, artificially supplied water in the form of bore-holes and gravel pits for road construction, have resulted in relatively high numbers of predators and scavengers. These anthropogenic factors have impinged on the natural system, masking the relationships between rainfall, food production and wildebeest numbers.

## SUMMARY OF BIOTIC FACTORS LIMITING WILDEBEEST (1964 TO 1994)

Because abnormal levels of anthrax and predation were identified by Berry (1981a) as major limiting factors for wildebeest, mortality records were analyzed in regard to confirmed and suspected deaths from anthrax and confirmed kills by large carnivores (Tables 2 and 4). Prior to 1975, mortality records in Etosha concentrated mainly on disease-related deaths, and were recorded by Ebedes (1976). He found that Burchell's zebra, wildebeest, and springbok accounted for 96 % of all anthrax-positive mortalities during the 10-year period 1964-74. Ebedes' (1976) findings were biased towards large plains-dwelling herbivores which died of anthrax. During the subsequent 20 years (1975-94) when mortalities throughout Etosha were taken into account, Burchell's zebra remained the species most affected by anthrax (39 %), however anthrax in elephants increased sharply to 27 %, followed by wildebeest at 21 %.

Preferred prey species of lion on the grasslands from 1975-78 (Berry 1980) ranked wildebeest first, followed by gemsbok, Burchell's zebra, springbok and ostrich. Similar to Ebedes' (1976) study, Berry's (1980) report accented the plains-dwelling herbivores, thereby biasing the results. However, because the decreases in both wildebeest and zebra numbers have made them relatively unavailable to predators, mortality records since 1978 indicate that kudu and giraffe, both woodland dwellers, have become the preferred prey species of large predators (Table 4).

No investigation into wildebeest nutritive status has been done since 1978 but, despite the prevalence of drought conditions since 1979, wildebeests' external condition appeared good in the majority of the population. Moreover, in the absence of recorded mortalities in wildebeest which could be ascribed to malnutrition or thirst, it appears that neither food or water played a significantly limiting role subsequent to the detailed study which ended in 1978.

TABLE 4: Seven preferred major ungulate prey species of lion, cheetah, spotted hyaena, leopard and black-backed jackal in the Etosha National Park (1975-93), occurring in areas inhabited by wildebeest. n = 1 253 records. Sources of data: mortality records at Etosha Ecological Institute, Okaukuejo.

| Prey species | No. of kills recorded | Relative kill frequency (%) | Relative abundance of prey (%) * | Prey preference rating ** |
|---|---|---|---|---|
| TS | 137 | 10,9 | 3,8 | 2,86 |
| GC | 67 | 5,3 | 4,5 | 1,18 |
| EB | 329 | 26,3 | 22,6 | 1,16 |
| TO | 21 | 1,7 | 1,5 | 1,13 |
| AM | 489 | 39,0 | 43,5 | 0,90 |
| CT | 112 | 8,9 | 10,1 | 0,88 |
| OG | 99 | 7,9 | 14,0 | 0,56 |

TS = *Tragelaphus strepsiceros*, GC = *Giraffa camelopardalis*
EB = *Equus burchellii*, TO = *Taurotragus oryx*, CT = *Connochaetes taurinus*, AM = *Antidorcas marsupialis*, OG = *Oryx gazella*

* Relative abundance of prey was calculated from the results of the 1982, 1984, 1987 aerial total censuses and the 1990 aerial sample census.

$$\text{** Prey preference rating} = \frac{\text{Relative kill frequency}}{\text{Relative abundance of prey}}$$

## RECOMMENDATIONS FOR MANAGEMENT OF WILDEBEEST IN ETOSHA

To counter the situation existing for wildebeest in Etosha, recommendations were based on practical considerations. Two major options existed in 1978: either modify Etosha's boundaries or attempt to manage within the existing boundaries.

### Modification of Etosha's existing boundaries

This was aimed at incorporating some of the original habitat of the previous migratory wildebeest population, as well as other migratory species. Essentially this would include two adjoining natural features which lay in what was then Owambo to the north of Etosha. One is the plains system surrounding Lake Oponono; the other, to the east of this, is the Andoni plains system of which the majority lies outside Etosha (Figure 4). Without these 2 areas, a semblance of the former migratory routes could not exist

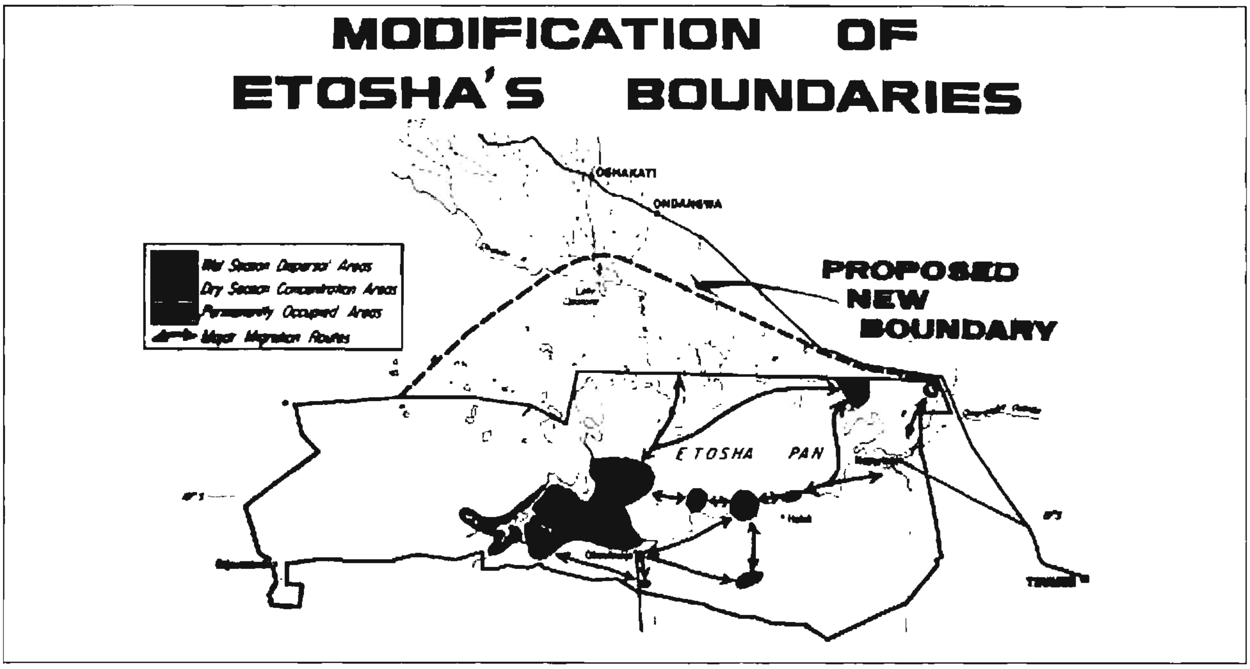


FIGURE 4: Modifications to the boundary of Etosha National Park which were proposed in 1980. The modification was aimed at incorporating the area from Lake Oponono southwards into Etosha, as well as the Andoni area to the south-east of Lake Oponono.

and the previous numbers of plains-dwelling ungulates were unlikely to be regained. However, any boundary changes to Etosha would have affected political geography and have required consensus at the first tier of what was then a South African government. As a result, factors which were beyond the scope of the study were involved. A submission was nevertheless made to the authorities that an expansion of the Etosha conservation area to encompass the Andoni-Oponono region would favour the migratory herds. Moreover, it was stated that this increased area of conservation could then be "**managed to the benefit of the Owambo people through tourism and possibly wild animal cropping on a sustained yield basis**". The additional observation was made that "**the present situation is an impasse which may result in further reductions of wildebeest and other large herbivores in Etosha**".

### Management within Etosha's present boundaries

It was considered essential, not only in the case of wildebeest, but for most other large herbivore species as well, to counter the imbalance caused by abnormal levels of disease and predation. Burning of anthrax-infected carcases, and the closure of gravel pits or their isolation by fencing, as was then being attempted, was not recommended since none of these methods can be effective in an area the size of Etosha. It was instead recommended that the anthrax problem be approached by combined research of veterinarians and ecologists, using the expertise of applied mathematicians to assist in building predictive models for anthrax epizoötics in Etosha.

Also, the closure of specific artificial water sources on the plains of Etosha was recommended. These were: Adamax, Leeubron, Gaseb and Gemsbokvlakte in the Okaukuejo area, because they provided permanent drinking places for both large herbivores and their attendant predator-scavengers.

It was furthermore firmly recommended that no additional artificial water sources be made available to animals without supportive research results because the introduction of such drinking points in a semi-arid area like Etosha must take into account the periodicity of droughts, when primary food production may fail to meet the requirements of the herbivores. Degradation of the surrounding vegetation around artificial water supply was a further aspect emphasised in a separate study by le Roux (1980).

Finally, culling of lion and spotted hyaena in Etosha was not recommended, based on the undesirable results achieved when this was carried out during a similar situation in the Kruger National Park, South Africa (Smuts 1975-76, 1978a, b, c).

These recommendations were included in an original thesis on wildebeest (Berry 1980) but were never published because especially the boundary changes mentioned for Etosha were in conflict with the political dispensation at the time. A paper containing these recommendations was submitted for publication, but it was rejected on the grounds that they were inappropriate.

Although Adamax, Leeubron and Gaseb water-holes were closed, Gemsbokvlakte remained open. Recently (1992), a new bore-hole named Nebrownii was opened approximately 5 km north of the previous Gaseb, 9 km north-west of Gemsbokvlakte and 8 km east of Okaukuejo. Nebrownii is an experiment to relieve pressure on Okaukuejo and Gemsbokvlakte, due to the high number of animals, especially elephant, Burchell's zebra, gemsbok and springbok, which have denuded the vegetation. However, as proven in the case of previous bore-holes, the vegetation around Nebrownii is already showing degradation.

## SYNTHESIS OF THE 1975-78 STUDY (Berry 1982; Berry & Siegfried 1991)

Factors which have determined evolution in wildebeest, such as climate, habitat, food, water, disease and predation have placed them in the niche of highly specialised ruminants of African grasslands. In Etosha they survive in an environment predominated by sporadic, variable rainfall which produces short grass, high in crude fibre content. Their successful adaptation has been the result of significant but slow changes in the environment. It is consequently predictable that when wildebeest are confronted by the modern situation existing at Etosha, where equally significant, but very rapid and negative changes to the environment have been made by humans, these highly specialised ruminants will be among the first to suffer. This has proved to be the case: the previous wildebeest population has been unable to withstand the cumulative onslaught of fencing coupled with elevated levels of disease and predation, all of which can be related to human interference.

## CONCLUSION

The Etosha wildebeest population appears to be locked in an impasse of anthropogenic and natural pressures from which it is unable to recover. Human influences may be manageable to a limited extent, but cannot be erased because this would entail removal of fences around Etosha and in northern Namibia, plus closure of all artificially supplied water-holes and gravel pits for road-building. It would also entail protection from modern hunting methods.

The natural primary determinants of rainfall and plant production which govern Etosha's wildlife are not controllable, while the two major biotic pressures of disease and predation remain critical for management of wildebeest and other large herbivores.

Etosha is no longer an environment in which wildebeest thrive and the possibility exists that the species may become endangered in Namibia. Their future is certainly threatened if present environmental conditions continue. To reinstate wildebeest as one of the major plains animals of Etosha, corrective management must clearly distinguish between cause and effect. Since treating the effect is at best a temporary measure, management will have to be at the causal level.

Consequently, the approach to solving Etosha's wildebeest problem should be to mimic the previous natural order in this semi-arid environment; if this is not done, there is little chance of success. One method of achieving this is to create viable conservation areas adjoining Etosha's borders which could later be linked to Etosha by migratory passages. Reducing the impact of proximal limiting factors could nevertheless be considered as an interim measure to prevent short-term catastrophic declines of the remaining wildebeest population.

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