

# The wildebeest problem in the Etosha National Park: a synthesis

by

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## 1 INTRODUCTION

In order to understand why the present environment in Etosha has changed to the detriment of the wildebeest population (Berry, 1980), it is helpful to consider the factors which shaped the evolution of ruminants and, in particular, African antelope. The primary determinants of food, water, climate, disease and predation which changed the environment, consequently made niches available to different species. The inter- and intraspecific competition which developed from niche overlap were the mechanisms by which biological change occurred. In addition, the reproductive adaptations of species which evolved had a profound influence on the ability to survive a changed environment. With these considerations in mind, I intend to synthesise the implications of my findings in relation to wildebeest.

## 2 EVOLUTIONARY HISTORY OF AFRICAN UNGULATES

Although the first well-defined Artiodactyla can be traced back to the Eocene, approximately 35<sup>6</sup> – 55<sup>6</sup> yrs BP, the fossil record of Tertiary period mammals indicates that African ungulates appeared 12<sup>6</sup> – 25<sup>6</sup> yrs BP during the Miocene (Cooke, 1972). The environment of the forerunners of these early ungulates was probably more equable than it is now, in regard to topography, climate and vegetation (Moreau, 1952). According to Cooke (1958, 1972), Africa's landscape during the Eocene-Oligocene was topographically monotonous, rising gradually from sea level to a highland of less than 1 700 m. Mean temperatures may have been higher than the present (Dorman and Gill, 1959) and the con-

## ABSTRACT

The evolutionary time span required to produce specialist grazers such as wildebeest is considered in relation to the effect on the species of rapid, man-induced changes in Etosha, such as fencing, constructed water points and abnormal levels of disease and predation. Basic environmental requirements for a viable wildebeest population are examined and related to the situation presently existing in Etosha.

continent was well-watered, giving rise to areas of forest interspersed with savanna (Cooke, 1972).

With the advent of the Miocene, the ungulate fauna included essentially African Bovidae (Gentry, 1968) and were equipped with typical hornlike organs (Geist, 1966). These early bovids commenced to diversify at the generic level in a climate where temperatures were still above the present and rift faults plus volcanic activity changed the formerly even topography of north and east Africa (Cooke, 1972). Based on evidence from oceanic cores, Siesser (1978) suggests that a major cooling and upwelling of the Benguela current in the late Miocene (c.  $10^6$  yrs BP) initiated aridification of the Namib Desert in the south-west of Africa.

It appears, however, that the central and east African vegetation during the Miocene was basically similar to the existing woodland-savanna environment (Chaney, 1933). Declining temperatures coupled with topographical elevations in the Oligocene-Miocene should be viewed as primary causes of the emergence of distinct climatic zones and a considerable extension of the savannas (Cooke, 1972). These in turn favoured the adaptive radiation of ungulates.

The Pliocene ( $3^6 - 12^6$  yrs BP) was characterised by further topographical uplifting coupled with volcanic activity (Cooke, 1972). These geological events had a pronounced climatic effect on the entire continent, with desertification taking place in the Saharan and Kalahari areas (King, 1962). The Bovidae by now included alcelaphine forms whose great diversity, as shown by fossil records, supports the hypothesis that they were essentially African in origin (Wells, 1957).

Pleistocene fossil faunas of Africa indicate that this successful radiation of ungulates continued (Cooke, 1963). However, a considerable number of bovid species, notably the alcelaphines, became extinct, probably due to their inability to adapt to climatic change which accompanied the alternating glacial-interglacial periods of the Pleistocene (Cooke, 1972). Nevertheless, it is highly probable that the Bovidae underwent a considerable diversification during the stresses imposed by Pleistocene climate and that they were completely differentiated to the generic level at the beginning of this period (Wells and Cooke, 1957). If this history of changing habitat and its effect on the evolution of African ungulates is related to the present situation, the dominance of the Bovidae with 78 extant species (Bigalke, 1972) can be satisfactorily explained.

Understandably, the literature contains no reference to the role of disease and parasites in the vertebrate faunas during the Tertiary-Quaternary, but the pressures exerted by predation are evident. The early carnivores, in the form of Hyaenodontidae, evolved at the start of the Oligocene (Cooke, 1972) and so preceded the Bovidae. Thus the bovids were probably subjected to considerable predation during their Miocene development when the Canidae, Viverridae and Felidae were established (Savage, 1965). The Hyaenidae consolidated

the role of predators during the later Pliocene (Hendey, 1970).

In summary, it is apparent that the present African bovids have prehistoric origins and that their evolution has been shaped by environmental pressures exerted on ancestral forms over millions of years. Their present diversity, which is unparalleled by any community of large, terrestrial mammals in existence (Bigalke, 1972), is the result of successful adaptation to significant but slow changes in the environment. It is important to the present situation confronting wildebeest in Etosha and elsewhere in Africa that the time span required to produce ungulates as highly specialised as wildebeest must be taken into account when evaluating the effect of a rapidly changing, modern environment in which man has the greatest impact.

### 3 ECOLOGICAL SUCCESS OF AFRICAN RUMINANTS

Here I use the term "ruminant" for any artiodactyl that ferments cellulose in its stomach. The success of ruminants, and in particular the Bovidae, has been due to their ability to adapt to long term environmental changes. These adaptations have enabled them to colonise most of the habitats which developed in Africa. It is generally accepted (Keast, 1968, 1972; Bigalke, 1972; Jarman, 1974; Sinclair, 1977) that vegetation is the all-important factor in terrestrial herbivore biology, providing food, water, shelter from unfavourable climate and protection from natural enemies. Following Davis' (1962) classification of six biotic zones in Africa, it is clear that bovids have successfully colonised the entire African continent.

Bigalke (1972) draws attention to the fact, however, that the basic dichotomy in extant bovids can be made between forest and non-forest forms, a difference extending back to the ancestral ungulates which inhabited the woodland-savanna mosaic of the Oligocene (Cooke, 1972). For the purpose of this synthesis I intend to examine the situation relating to savanna antelope only.

The mechanisms which enable Africa to support 78 bovine species have been listed by Keast (1972) who comments that savanna predominates in Africa, supporting 80% of the bovine species. Furthermore, antelope communities exhibit the greatest number of species and produce the greatest biomass in grassland and savanna, both factors being attributable to their manner of feeding, food digestion and their group size which are coupled to anti-predator behaviour and social organisation (Jarman, 1974).

To achieve this adaptive radiation, the bovids inhabiting savanna evolved several major characteristics which remain vital to their survival in an environment characterised by short, unreliable rainy seasons, producing grass with high levels of crude fibre. These are:

- (i) The development of a capacious rumen which enables the diet, comprising mainly grass cellulose of low digestibility, to be effectively converted by microbial action into protein and digestible carbohydrates. Rumen bacteria are also able to synthesise vitamin B complex, making the ruminant relatively independent of an external source. Furthermore, the ruminant stomach allows the recycling of non-protein nitrogenous substances, in the form of urea, to take place effectively via the blood and the saliva. Urea conservation is further advantageous in that it assists ruminants to conserve water since excreted urea requires a certain amount of water (Schaller, 1967). In common with other ungulates, ruminants can accumulate large amounts of carotene during the nutrient flush in plants, for storage as vitamin A in the liver, and they effectively synthesise vitamin C. Thus the ruminant is able to contend very satisfactorily with the erratic supply of nutrients produced by a capricious environment.
- (ii) The evolution of a quadri-tubercular mouth morphology with blade-like lower incisors and canines designed for rapid cropping and ingestion of the forage for subsequent reduction by chewing the cud with grinding, molariform teeth. This adaptation has been described as the "eat and run" phenomenon which favours predator avoidance (Janis, 1976) and also thermoregulation, in that ruminants are able to move from open grazing areas and shade from direct solar radiation during the digestive processes.
- (iii) The specialised limb morphology in artiodactyls by way of a unique, double trochleated tarsal joint which has contributed to their survival by allowing escape from predators through extremely rapid acceleration (Janis, 1976).
- (iv) The development of horns, which in males, and sometimes females, can be effectively used to counter predator attacks and also in inter- or intra-specific attack/defence situations (Leuthold, 1977). In those ruminants having curvature of the horn cores, such as alcelaphines, a further advantage exists in bringing the centre of gravity closer to the head, thereby favouring balance during flight situations while retaining horn strength (Vrba, 1971).
- (v) The evolution of a large body size in the majority of species which resulted in more effective long distance locomotion coupled to energy conservation. The latter is well-illustrated by Benedict's (1938) "mouse to elephant curve". These large savanna-dwelling ruminants were able to develop migratory habits which enabled them to search for and find the best quality forage during the brief rainy periods which characterise large areas of Africa's grassland savannas.
- (vi) The high degree of development of the neo-cortex of the telencephalon, which is linked to a

trend in greater social organisation and a change from browser to grazer (Oboussier, 1979). This brain development is also correlated with specialisation of the structure of the stomach as well as the morphology of the lower jaw. The strong social characteristics exhibited include territorialism which is advantageous in tropical regions where reduced seasonal forage surpluses favour high local population densities (Owen-Smith, 1977).

Thus, if these major characteristics, most of which are unique to ruminants, are considered, it is not surprising that they, and in particular the Bovidae, have achieved far greater success in their adaptive radiation than the Equidae. There are 78 bovid species as opposed to five equid species in Africa (Kest, 1972).

Dissension about the so-called "inefficiency" of digestion in equids has been voiced by Janis (1976) who maintains that caecal fermentation is superior to the ungulate rumen for dealing with a high crude fibre content in the forage. It is acknowledged that ruminants are less efficient utilisers of energy and protein than non-ruminants (Reid, 1970; Smith, 1975; Owens and Isaacson, 1977). Consequently, if the mechanism of the rumen, namely pregastric fermentation, is viewed against Hutchinson's (1957) concept of "niche", then it becomes evident that the microbial-mammal symbiosis which exists in the ruminant leads to expansion of the realised nutritional niche, as argued by Kinnear *et al.* (1979). They furthermore pose the hypothesis that ruminant and ruminant-like mammals occupying these relatively less nutritious, expanded niches largely avoid competitive overlap for food by herbivores possessing different digestive systems. What emerges then from these debated points is that the successful colonisation of Africa's grassland savannas by ruminating herbivores has probably been brought about by the principle of competitive exclusion. By including a microbe component in their digestive processes, ruminants have had to concede one trophic level to their internal symbionts, thereby lengthening their food chain and lessening their energetic and productive efficiency (Kinnear and Main, 1975). They have gained advantageously, however, by being equipped to occupy expanded, but less nutritious niches. In so doing ruminants avoid competition by excluding other mammals with different alimentary systems.

#### 4 EXISTING ENVIRONMENTAL CONDITIONS FOR WILDEBEEST IN ETOSHA

With these foregoing considerations in mind, I will now relate the basic requirements of a typical savanna-dwelling ruminant, namely wildebeest, to the situation existing in Etosha, as evidenced by the present investigation (Berry, 1980).

#### 4.1 Water requirements

Being a bulk and roughage grazer of grass and therefore dependent on water, wildebeest in Etosha exhibited a daily drinking pattern during 94% of observations. This obligation to drink was further underlined by their kidney function which, although relatively efficient, did not show reduced water loss via the urine during the dry season. This was demonstrated by insignificant seasonal differences in urine osmolality. Their dependence on water confined wildebeest to a measured grazing radius of 15 km from drinking places and although neither water quality nor quantity were limiting during my study, it is predictable that wildebeest will be the first large herbivore species to suffer during a drought when the water-food link becomes critical.

Wildebeest in Etosha have therefore enjoyed the advantages of specialist grazers during the past five years, a period of above average rainfall and good forage production. However, the fencing of Etosha was completed at the start of this period and the wildebeest have not yet had to cope with a drought under fenced conditions. If successive drought years were to prevail then the water-food demand in wildebeest may not be met by the relative availability of these two critical factors. Unable to migrate out of Etosha, the species may well be faced with the choice of dying of thirst or of hunger.

#### 4.2 Food requirements

At least 97% of the diet of wildebeest in Etosha consisted of grass. This they grazed selectively, having up to 75% of nutrient-rich grass leaf and grass sheath in their rumen during the wet season. Proximate analysis of the forage available to wildebeest showed high crude protein levels (18%) in the wet season, declining to 4% during dry season dormancy. Thus, although there may have been a marginal shortfall of crude protein at the nadir of grass production, the feeding selectivity of wildebeest, their ability to circulate urea via the blood and saliva, and to synthesise protein in the rumen by microbial action, make it likely that no real protein deficiency existed at any time of the year. Similarly, the soluble carbohydrate content of the grass (46 – 61%) ensured an adequate supply of highly digestible energy to wildebeest. In addition, the crude fibre present (27 – 34%) constituted an additional source of energy through the ability of symbiotic flora in the wildebeest's rumen to transform cellulose into energy-producing, volatile fatty acids. Thus, during the period of study, the energy/protein supply of Etosha's grasslands was sufficient to meet the demands of wildebeest and other large herbivores. Phosphorus, copper and cobalt may have been marginally deficient in the diet, but there was no evidence of this in the nutritional status of the wildebeest, which was demonstrably good. Consequently, nutrition was not limiting to the population during the period 1974 – 78, but because of

the food-water link in wildebeest nutrition, a critical shortage of available nutrients may occur during a protracted drought.

#### 4.3 Reproduction

The high pregnancy rate in adult wildebeest cows in Etosha ( $\bar{x} = 87\%$ ) is a further criterion for assuming that nutrition was adequate. The synchronised nature of wildebeest calving, which occurred during the peak rain period of January-February, indicated that the demand for protein by reproductive females has adjusted to the seasonal supply of this critical nutrient. The quality of wildebeest milk was further confirmation of the nutritional adequacy of the grass. Milk levels of protein and fat greatly exceeded those of domestic cattle while gross energy value of wildebeest milk was 6,14 J.g<sup>-1</sup> compared to 2,91 J.g<sup>-1</sup> in dairy milk. Although there appears to be a negative correlation between the amount of energy invested in reproduction and the subsequent survival or reproductive performance of the parent, specific nutrients such as nitrogen may be more important to the cost of reproduction (Calow, 1979). Considering this and taking into account the levels of energy and protein in the available forage, their relative levels in the milk, the high pregnancy rate and good nutritional status of pregnant cows, it was evident that Etosha's wildebeest were reproducing satisfactorily. Consequently, reproductive ability could not be a factor contributing in any significant way to the decline in wildebeest numbers.

#### 4.4 Climatic factors

Wildebeest in Etosha were able to adapt successfully to heat and cold by shading, panting and orientation of the body to the sun and wind. The details of these observations will be reported elsewhere (Berry *et al.*, in prep.). Nevertheless, for the sake of completeness it can be stated that Etosha's climate was not considered to be limiting for wildebeest.

#### 4.5 Disease and predation

Apart from anthrax, no other major disease was diagnosed in Etosha's wildebeest. Anthrax featured prominently during all seasons in Etosha, with a peak during the wet season when 76% of the known mortality in wildebeest was due to anthrax. The endemic status of anthrax has been achieved by the establishment of "incubator areas" for the sporulated phase of the disease in alkaline gravel pits created for road-building. Under the ideal conditions which exist in Etosha for anthrax, epidemics occur fairly predictably during the rainy season. Etosha's carnivores are apparently not susceptible to anthrax and have, moreover, benefited from the food supply provided by anthrax-infected carcasses. Additional stability for the major carnivores,

especially lion and spotted hyaena, has been provided by artificial water points and carnivores can now inhabit the entire grassland area permanently. Initial estimates gave lion-prey ratios of 1:107 – 153 and combined predator-prey ratios of 1:72 – 105. These ratios show that Etosha has, on average, 1.7 times the live mass of predator to prey than other areas of Africa. Furthermore, wildebeest were a major prey species for lion and hyaena. Together then, the combined pressures of disease and predation are seen as the major factors in the reduction of wildebeest numbers during the period 1974 – 78, although earlier decreases may have been caused by the added effects of drought.

During the study, adult mortality, as evidenced by tooth attrition in a sample of 283 skulls, was highest between three and six years of age (48% of all skulls found). By 10 years of age 91% of all adults had died. This early adult mortality was more severe than in other declining wildebeest populations. A computer model which simulated the demography of the population and predicted trends between 1973 – 82, showed that 260 – 700 wildebeest older than one year died annually and that this mortality exceeded the recruitment rate of sub-adults to the breeding stock.

## 5 CONCLUSIONS

During the course of my investigation it became evident that man's activities are basically responsible for the decline in wildebeest numbers. The initial impact on the former migratory population was fencing erected along Etosha's boundaries and elsewhere outside the park. Some of these fences were veterinary cordons, 2.5 m high and well-maintained. They virtually eliminated the ability of the species to migrate, especially during droughts. When Etosha was fenced, wildebeest and most other large free-ranging animals which were outside the park at the time, were progressively decimated by a combination of hunting and competition with expanding populations of man and his domestic stock. The stage is now reached where the former migratory population of *c.* 25 000 wildebeest has been eliminated. It is true that Etosha's boundary fence is almost never totally intact because of the vagaries of an expanding elephant population. Elephant fence-breaking, however, takes place mostly in the woodlands of Etosha and the portions of the fence which span the grasslands are seldom affected. Such breaks are conspicuous and are repaired rapidly. The plains animals are consequently effectively fenced in. Moreover, with the expanded human settlements which surround Etosha, most wildebeest which manage to leave the sanctuary of the park are killed by hunting and therefore lost in any event.

The extermination of the large migratory herds was the first phase in the reduction of wildebeest numbers in South West Africa. The remaining population of *c.* 4 000, which was confined to Etosha by fenced boundaries in 1973, was further subjected to other man-made

factors in the form of artificial water points and gravel pits for road-building. The former expanded and stabilised the predator-scavenger component; the latter created incubator areas for anthrax bacilli. The effects of abnormal levels of disease and predation on wildebeest and other large herbivores have been quantitatively demonstrated by Berry (1980). I wish to reiterate that since the closure of Etosha by fencing, the resident wildebeest population has not been subjected to a prolonged drought. As discussed earlier, the food-water link in wildebeest is critical and if drought conditions were to prevail, the population would be subjected to additional environmental pressure.

## 6 SUMMARY

The factors determining evolution in wildebeest, such as food, water, climate, disease and predation, have been examined and it has been concluded that their present position as highly specialised ruminants of the African grasslands is the result of successful adaptation to significant, but slow changes in the environment.

Wildebeest achieved adaptive radiation by developing several major characteristics which are vital to their survival in an environment predominated by short, unreliable rainy seasons, producing grass high in crude fibre content. These specialised characteristics are:

- (i) a rumen wherein symbiotic microflora converts cellulose to protein and carbohydrates, and also synthesises vitamin B complex. In addition, the rumen permits recycling of urea via the blood and the saliva.
- (ii) a mouth morphology designed for rapid cropping and ingestion of grass which favours predator avoidance and thermoregulation.
- (iii) a specialised leg morphology which also favours predator avoidance.
- (iv) the development of inward-curving horns which aid balance and can counter predator attacks
- (v) a large body size which aids long distance trekking
- (vi) a highly developed neocortex in the brain which is correlated with social organisation, a tendency to graze instead of browse, and specialisation of stomach and mandible morphology.

Nevertheless, by including a microbe component in their digestive processes, wildebeest must concede one trophic level, thereby lengthening their food chain and lessening their energetic and productive efficiency. This system has the advantage, however, of allowing wildebeest to occupy expanded food niches.

When these environmental requirements of wildebeest are related to the situation existing in Etosha, it becomes evident that they will be the first large herbivore to suffer when drought conditions prevail. Furthermore, because wildebeest are obligate drinkers, the food-water link will become critical during drought. The calving rate and milk quality of wildebeest during the stu-

dy, a period of above-average rainfall, was normal. Also, the birth of calves was highly synchronised with the rains and the accompanying nutrient flush in grass. Similarly, wildebeest have adapted well to the climatic extremes encountered in Etosha by shading, panting and orientation of the body to the sun and wind.

However, when the environmental pressures exerted by disease, especially anthrax, and predation, notably by lions, were examined, it was evident that in combination they were responsible for more wildebeest mortality during the study than any other causes.

Man's activities are considered to be basically responsible for the drastic decline in wildebeest numbers. Initially, the boundary fence around Etosha and veterinary barriers outside the park eliminated the ability of the species to migrate. This severely decimated the original population. Subsequently, the residual population remaining within Etosha has been subjected to elevated levels of anthrax caused by "incubator areas" in gravel pits used for road-building. The abundant supply of anthrax-infected carcasses during an epidemic favours lions and other carnivores which are immune to anthrax. Man has further stabilised the environment for predators by constructing artificial water points.

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