

Population structure, mortality patterns and a predictive model for estimating future trends in wildebeest numbers in the Etosha National Park

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1 INTRODUCTION

The aim of this investigation was to estimate the total population of wildebeest *Connochaetes taurinus* in Etosha, to examine its structure, and to identify the factors which may have caused a decline in numbers.

1.1 Decline in total population

Prior to aerial counts which commenced in 1966, only general estimates of the wildebeest population in the Etosha National Park were made. These ranged from 20 000 to 30 000 wildebeest in 1913 (Jaeger, 1926-1927), 7 000 to 10 000 in 1952 (Schoeman, 1952), 25 000 in 1954 (De la Bat, 1977 pers. comm.) and 30 000 in the period ending 1965 (Viljoen, 1967). In 1966 the aerial counts were carried out in limited time and no population estimates were possible (Ebedes *et al.*, 1967). The first dry season aerial census in September 1968, when water dependent species occupied "dry season concentration areas" (Bigalke, 1961), gave a total of 4 073 wildebeest (Ebedes, 1968). According to Ebedes (1977, pers. comm.), he undercounted by 10-20 % and estimated the total population at 5 000. In April 1969 and February 1970 aerial strip counts were flown for the first time over Etosha and were subsequently adopted in preference to the previous method of random counting. Thereby 4 773 (1969) and

ABSTRACT

Following a decline in the wildebeest population from 25 000 to 2 500 between 1954-78 it was established that the calving percentage was normal (22 % of total population) but that disproportionate mortality, favouring the cows, resulted in 48 % of recorded deaths between 3-6 years of age. By 10 years of age 91 % of all adults had died. Disease, namely anthrax and abnormal predation levels caused this high death rate. A computer model predicted that with a birth-rate of 0.35, a calf survival rate of 0.5 and a yearly kill rate of 1.25-2.5 wildebeest per adult lion, the wildebeest population would remain at its present level of 2 500.

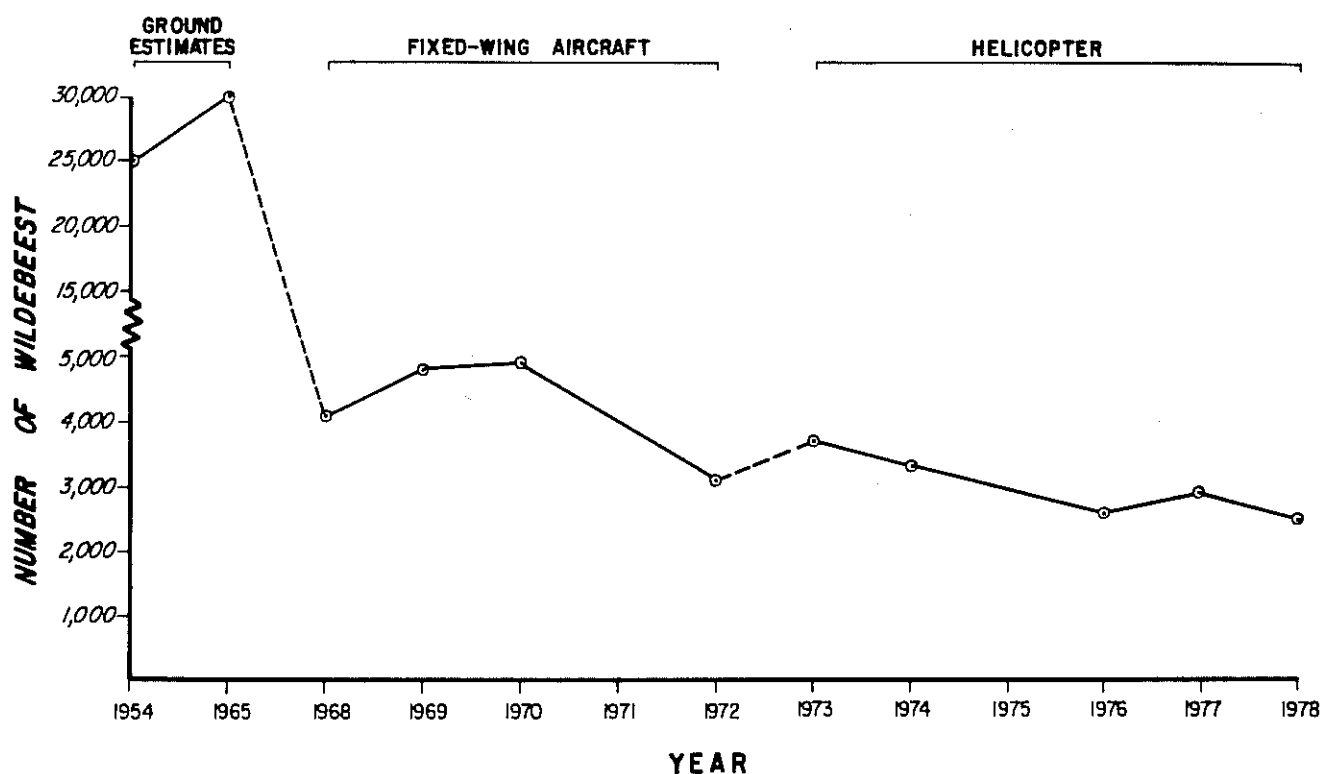


FIGURE 1: Estimates and aerial counts of the wildebeest population in Etosha between 1954 and 1978.

4 789 (1970) wildebeest were counted (Ebedes *et al.*, 1970), but the increase over previous years was considered to be a result of the improved method. Nevertheless, fixed-wing aircraft have disadvantages, such as limited view and turning ability, when compared to a helicopter. This became evident when the first census of the Etosha plains was undertaken by helicopter in September 1973 (Joubert *et al.*, 1973). They counted 3 717 wildebeest, an increase of 21 % over the October 1972 count of 3 078 (Du Preez, 1972). The subsequent counts I did by helicopter (1974–1978) revealed a declining population of which the numbers dropped from 3 300 to 2 493 (Berry, 1978). The decreasing trend is Fig. 1.

1.2 Spatial and temporal distribution

The seasonal distribution of the wildebeest population is illustrated in Fig. 2 and reflects the strong influence of rainfall which resulted in dispersal over a large area between January and April (wet, hot season) and subsequent concentration around perennial water sources between May and December (dry, cold and dry, hot seasons). During my investigation (1974–1978) the population was divided into two discrete units. The westerly unit near Otjovasandu comprised one mixed herd of up to 27 animals plus a few solitary bulls which grouped periodically into a bachelor herd. Due to the isolated nature of the westerly unit and because they inhabited terrain which made them difficult to locate, my

observations were limited to aerial census and occasional sightings by vehicle. They appeared to be more stable in numbers than the much larger, declining population in the eastern sector of Etosha. The latter constituted 99 % of the total population and was concentrated in two areas, namely the Namutoni sub-unit and the Okaukuejo–Halali sub-unit (Fig. 2). Although some interchange occurred between these groups they occupied discrete areas.

2 METHODS

2.1 Aerial census of total population

A total of five censuses using a Hughes 300 C helicopter and a total of three censuses using a Piper Super Cub fixed-wing aircraft were made in the period 1973–78. On average, about 30 hours' flying time by helicopter was required to adequately census the area inhabited by wildebeest, and about 15 hours was needed by fixed-wing aircraft. Wildebeest were counted individually in herds numbering up to 20, and 35 mm photographic transparencies were taken of larger herds for subsequent projection and counting. In relatively small numbers, such as those encountered in Etosha, wildebeest are considered to give reliable counts from a helicopter, with close to 100 % sighting, especially with slow flight (Melton, 1978a, b). Since his results were obtained in the thickly vegetated Umfolozi Game Reserve

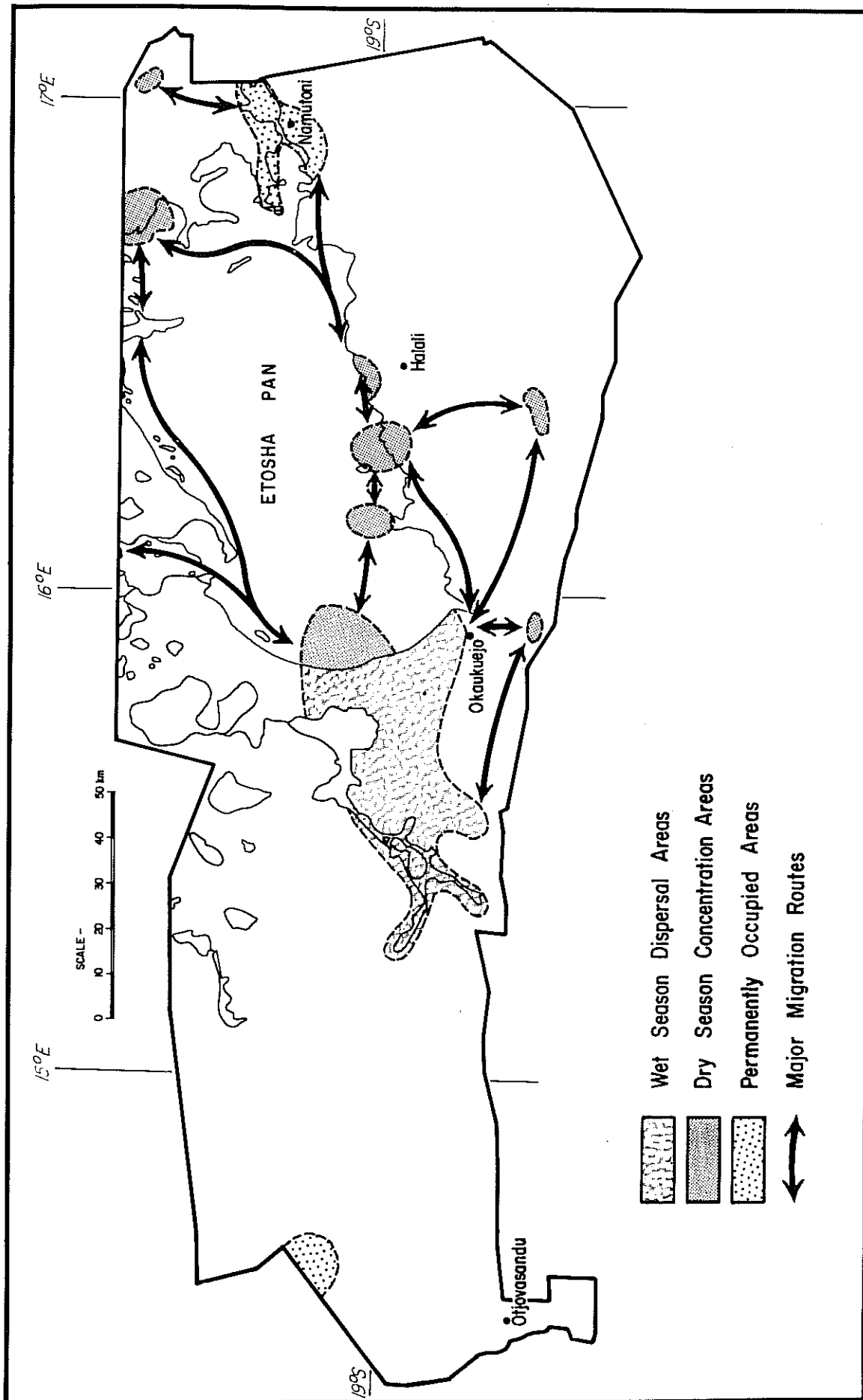


FIGURE 2: Seasonal distribution and major migration routes of the wildebeest population in Etosha (1974-78).

in Zululand, I considered the open grasslands and comparatively sparsely vegetated thorn savanna which wildebeest inhabit in Etosha to give very close to 100 % sightings of the population. Consequently no upward adjustment of the census figures was made. During aerial censuses I also noted the number of calves, the number of lone, territorial bulls and bachelor herd bulls, as well as the number of neck-banded animals sighted.

2.2 Ground observations for age—sex ratios

Observations on whole herds were made to establish age—sex and social status. Because of the synchronised nature of calving it was possible to identify up to four age classes, namely 0—1 year, 1—2 years, 2—3 years and adult. Sexing of wildebeest is relatively easy, but requires practice (Watson, 1967), and needs no further explanation. I was able to distinguish between mixed herds and bull herds, thereby obtaining a confirmation of the proportion of bull herds found in the population during aerial census. During the dry season when wildebeest concentrated at perennial fountains, a large and representative sample (31 %) of the population could be aged and sexed during any one day. This was facilitated by the good visibility at fountains on the edge of the Etosha Pan and by the habit of wildebeest to approach water in file. In this way it was possible to distinguish up to nine age classes during ground observations while a tenth class, namely lone, territorial bulls, could be identified during aerial counts.

2.3 Age determination by tooth attrition

To establish mortality patterns in wildebeest, a total of 283 skulls was recovered from the areas occupied by the eastern population unit of Etosha. I made a chronological table of tooth eruption and infundibular attrition, based on data from Talbot and Talbot (1963) and the detailed investigations by Watson (1967) and Attwell (1977) into wildebeest age determination. Because investigation of incremental growth layers of cementum or dentine is time-consuming and not always infallible (Spinage, 1976), especially in older animals which experience root resorption (Watson, 1967), I did not attempt to relate growth layers to age.

Also, the deposition of dental layers may not all be related to tooth attrition; for instance, 18 % of the sample investigated by Attwell (1977) was considered unsatisfactory. Furthermore, there is uncertainty whether the deposition rate of dental layers is governed by seasonal factors such as nutrition (Smuts, 1974; Spinage, 1976) or is the result of an endogenous rhythm (Grimsdell, 1973). During my study 10 premolars and molars were sectioned, polished and examined for incremental growth layers under a dissecting microscope at 6—50× magnification. However, the manifestation of several errors in this technique, such as possible mis-

interpretation of accessory and double lines of growth, precluded its objective use and will require more detailed investigation. I therefore relied on tooth eruption sequence which provided an accurate means of ageing wildebeest up to three years. Infundibular attrition, used in conjunction with Attwell's (1977) data, gave a practical assessment of age classes above three years.

2.4 Predictive modelling

A preliminary model, based on the methods of Starfield *et al.* (1976) and Shiell and Starfield (1977), was tested on a Univac 1106 computer by changing critical parameters which may have influenced the population. The parameters tested were number of lions, yearly kill rate of lions, calf survival rate, and birth rate. The model was initiated with the earliest, reliable census figures and was run for 10 consecutive years (1973—1982) to obtain predictions for change in the wildebeest population. Field data for the period 1973—78 were used to adjust the model to existing situations.

3 RESULTS

3.1 Estimation of total population

The counts made by helicopter and fixed-wing aircraft are given in Table 1.

3.2 Age—sex ratios

Table 2 shows the range and mean yearly ratios of the age—sex and social status of wildebeest in Etosha. The range indicated change in a particular component of the population during the year and was a measure of mortality rate in calves, immatures and sub-adults. In the case of adult bulls the yearly range also reflected their seasonally changing social status.

3.3 Age—sex ratios in mortality

A total of 15 age classes from birth to approximately 14 years was distinguishable and 197 of the 283 skulls could be accurately sexed (Table 3). Although the allocation of yearly age classes to the sample of skulls must be treated with caution because of individual variation in the rate of tooth wear (Watson, 1967; Attwell, 1977) the data are accurate from birth to three years. From three years to 10 years of age there may be a variation of up to one year in the estimated classes and for wildebeest older than 10 years this variation could be up to three years. Nevertheless, the age—sex classes which are subjected to the greatest mortality are clearly evident in Table 3.

TABLE 1: Aerial counts of wildebeest in Etosha (1974–78)

Year	Month	Numbers counted					Total	Type of aircraft*
		Older than 1 year	Calves	Mixed herds	Bachelor herds	Lone bulls		
1974	July	2 574	726	2 108	396	70	3 300	H
1976	May	1 782	578	1 427	285	70	2 360	Fwa
1976	July	2 034	604	1 744	241	49	2 638	H
1976	Dec.	2 078	585	1 757	285	32	2 659	Fwa
1977	March	2 576	483	2 160	276	140	3 059**	H
1977	Sept.	2 613	356	2 365	230	18	2 969**	Fwa
1978	March	2 069	424	1 539	388	142	2 493	H
Mean		2 247	537	1 871	300	74	2 783	—
±SD		334	124	346	66	49	336	—

* H = Helicopter; Fwa = Fixed-wing aircraft.

** Population totals of 3 059 and 2 969 include herds of 423 and 281 wildebeest respectively, which were sighted in Owambo, adjacent to Etosha's northern boundary. They may have been emigrating or were potential immigrants.

TABLE 2: Structure of the wildebeest population in Etosha in regard to age, sex, reproduction and social status (1976–78)

Year	Criteria used	Ground counts			Aerial counts	
		n	Range %	Mean %	n	Total %
1976	Calves	1 995	14–27	24	2 638	23
	Immatures		9–15	11		64
	Sub-adults		7–10	9		
	Non-pregnant cows		4–10	8		
	Pregnant cows		24–30	26		
	Lone bulls		1– 3	3		2
	Herd bulls		2– 3	3		2
	Bachelor bulls		12–17	16		9
1977	Calves	2 453	14–26	22	3 059	16
	Immatures		13–20	18		69
	Sub-adults		11–14	12		
	Non-pregnant cows		1– 2	2		
	Pregnant cows		28–32	29		
	Lone bulls		1– 4	3		5
	Herd bulls		2– 3	2		3
	Bachelor bulls		10–15	12		9
1978	Calves	7 274	16–24	20	2 493	17
	Immatures		11–15	13		57
	Sub-adults		9–11	10		
	Non-pregnant cows		1– 5	3		
	Pregnant cows		28–32	30		
	Lone bulls		1– 7	5		7
	Herd bulls		2– 4	3		3
	Bachelor bulls		14–18	16		16

3.4 Wildebeest population model

The trend in the population total was simulated by applying realistic values for the model's selected parameters (Table 4). Thereby the population model totalled 2 501 in 1978 which was close to the final aerial count of 2 493 wildebeest. Having established this preliminary model I then "tuned" the data input as suggested by Starfield *et al.* (1976) to find which parameter levels would have to exist to maintain the population at its 1978 total (Table 4). Subsequently, I purposely altered

each major parameter by an increase of 10 % and a decrease of 10 % (Fig. 3) to predict the population trend until 1982. A similar procedure (Shiell and Starfield, 1977) was used on wildebeest and zebra population models to test the sensitivity of parameters in the Kruger National Park. In the case of Etosha's wildebeest these increases and decreases were realistic and could conceivably occur if predation, calf survival and reproductive success were favourably or unfavourably influenced. The model I used was kept relatively simple to avoid confounding the predictions (Starfield *et al.*, 1976).

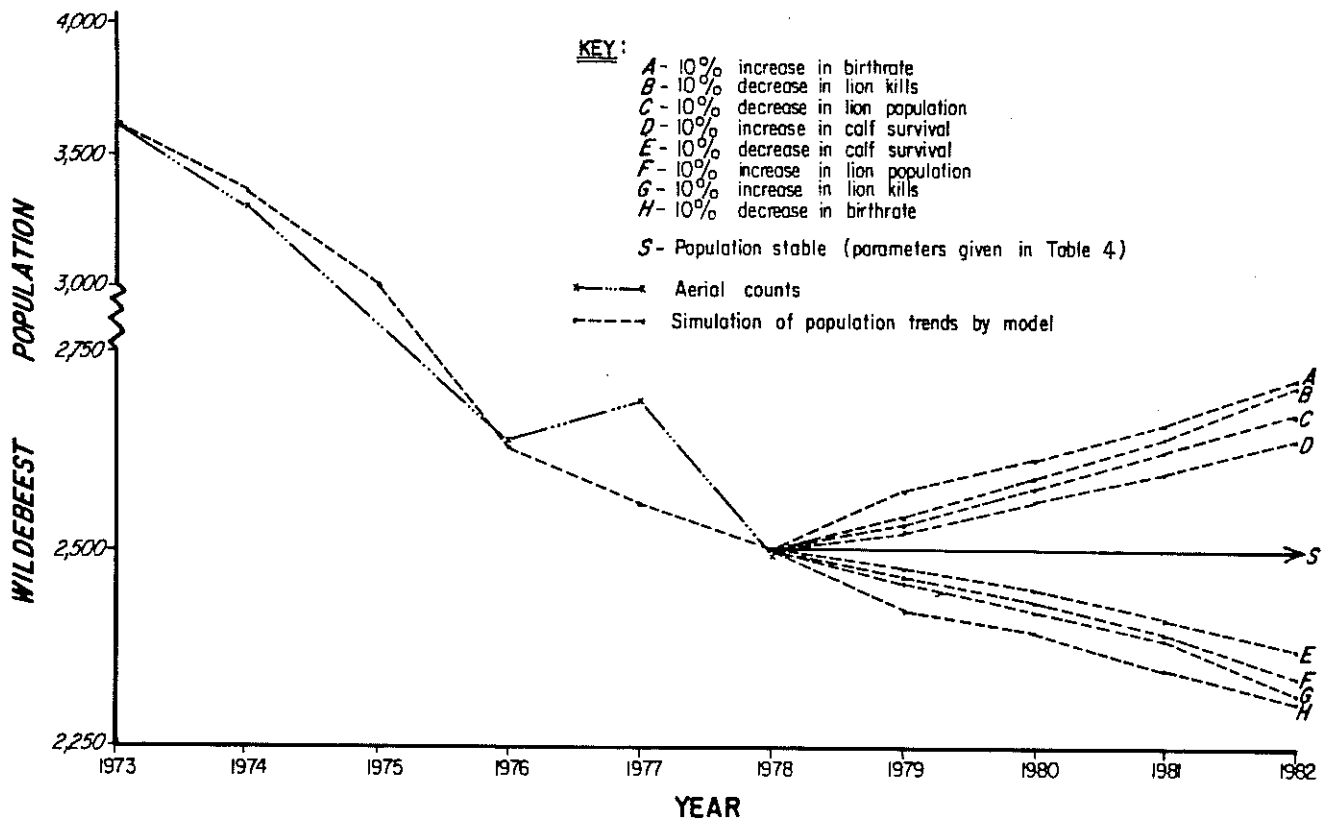


FIGURE 3: Wildebeest population model and predictions for future trends in Etosha (1973-82).

TABLE 3: Mortality patterns in wildebeest in Etosha (1976-78)

Estimated age in years	No. of skulls collected	Percentage of sample	Cumulative total*	Sex ratios		
				Bull	Cow	Total
0-0.5	1	<1	1	?	?	—
0.5-1.0	4	1	2	?	1	1
1-2	17	6	8	3	7	10
2-3	22	8	16	10	1	11
3-4	41	14	30	20	8	28
4-5	48	17	47	23	11	34
5-6	47	17	64	35	7	42
6-7	30	11	75	18	—	18
7-8	32	11	86	18	10	28
8-9	12	4	90	6	2	8
9-10	8	3	93	2	4	6
10-11	6	2	95	1	1	2
11-12	6	2	97	4	—	4
12-13	4	1	98	2	—	2
13-14	5	2	99	1	2	3
>14	0	0	100	0	0	0
Totals	283	100	100	143	54	197

* The cumulative total is biased in favour of adult skulls because of the rapidity with which carcasses of young animals are obliterated by predators and scavengers. Consequently the data cannot be used to establish a true age structure of the population.

TABLE 4: Simulation of Etosha's wildebeest population data, using various parameters (1973–82)

Year	Mean rainfall (mm)	Parameters				Results					
		Adult lion population	Kill rate	Calf survival rate	Adult birth-rate	Calves	Yearlings	2 Year olds	Adults	Total wildebeest population	Actual census figures
1973	250	280	2,50	0,5	0,35	743	483	372	2 119	3 717	3 717
1974	701	300	2,00	0,5	0,35	663	371	378	1 896	3 309	3 300
1975	424	300	2,00	0,5	0,35	621	332	272	1 774	2 998	No census
1976	577	256	1,25	0,5	0,35	534	310	252	1 525	2 621	2 638
1977	316	256	1,25	0,5	0,35	526	267	265	1 503	2 560	2 689
1978	590	208	1,25	0,5	0,35	523	263	219	1 496	2 501	2 493
1979	462	208	1,25	0,5	0,35	521	262	230	1 488	2 500	—
1980	279	208	1,25	0,5	0,35	522	260	227	1 492	2 502	—
1981	—	208	1,25	0,5	0,35	523	261	226	1 494	2 503	—
1982	—	208	1,25	0,5	0,35	523	261	227	1 494	2 505	—

TABLE 5: Population structure of the Etosha wildebeest population (1976–78), compared to a Zululand population investigated by Attwell (1977)

Criteria used	Area	
	Etosha*	Zululand**
No. of wildebeest sampled	3 907	800
Sample as % of population	31,0	30,0
% Lone, territorial bulls	3,7	9,0
% Breeding herd bulls	2,7	5,5
% Bachelor herd bulls	14,7	11,9
Mean size of bachelor herds	8,4	5,6
Range in size of bachelor herds	2–120	2–16
% Total full-grown bulls	21,0	26,4
% 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
% 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 counts (1976–78)

** Based on aerial count (August, 1974)

4 DISCUSSION

4.1 Population structure and mortality patterns

The structure of the Etosha wildebeest population was established by taking the mean of three years of ground counts (1976–78) which were considered to be more detailed and accurate than total aerial counts, except in the case of lone, territorial bulls where aerial counts were used (Table 2). Nevertheless, the aerial counts gave a reasonably similar population structure to that obtained from ground counts, thereby confirming that the ground counts were representative of the population. The detailed population structure is given in Table 5 and

I have chosen to compare it with the results of a similar investigation by Attwell (1977) which was, however, based mainly on aerial observations. This comparison attempted to establish which components of the two populations were similar, in view of the fact that Attwell (1977) estimated a 3,8 % decline in the population he studied.

From the data presented there appeared to be proportionately fewer full-grown bulls in Etosha and consequently relatively more adult cows in the population (1 bull : 1,57 cows in Etosha, compared to 1 bull : 1,49 cows (Attwell, 1977)). This suggests that bulls in Etosha were subjected to a higher mortality rate and is borne out by the sex ratio from skulls collected in Etosha (Table 3) which was 1 bull : 0,38 cows ($X^2 = 146,69$;

TABLE 6: Comparison of birth-rate and calf survival of wildebeest in Etosha with other populations.

Area	Mean seasonal rainfall (mm)	Criteria measured (mean)			
		Birth-rate		Calf survival	% Calves in total population
		2-year-olds	Adults		
Western Masailand East Africa ¹	762	0,83	0,95	0,20	19
Serengeti National Park Tanzania ²	782	0,37	0,96	0,24	10
Kruger National Park South Africa ³	584	0,32	0,92	0,34–0,70	15,4
Zululand South Africa ⁴	677	0,11	0,92	0,40	20,6
Wankie National Park Rhodesia ⁵	550	0,0	0,74	0,49	22
Etosha National Park South West Africa ⁶	469	0,0	0,86	0,50	22

¹ Talbot and Talbot (1963)² Watson (1967)³ Braack (1973); Starfield *et al.* (1976)⁴ Attwell (1977)⁵ Estes (1965); Higgins (1969)⁶ Present study

$P < 0,001$). In the Kruger National Park adult wildebeest sex ratios were more disparate (1 bull : 2,6 cows) which indicates an even greater mortality in bulls, probably due to a high rate of predation (Braack, 1973). Disproportionate mortality of males in free-ranging ungulate populations is a well established phenomenon (Watson, 1967; Estes, 1968; Mentis, 1972; Crowe and Liversidge, 1977; Hamilton *et al.*, 1977; Sinclair, 1977). Moreover, increased mortality in adult bulls is, in turn, an indicator of predation pressure (Schaller, 1972) and lone, territorial bulls may be particularly vulnerable to predation (Watson, 1967; Estes, 1968). Thus, when it is considered that lone bulls made up only 3,7 % of the Etosha population compared to 5,0 % in the Kruger National Park (Braack, 1973) and 9,0 % in Zululand (Attwell, 1977), it is apparent that predation was a significant factor in Etosha's bull wildebeest mortality. This higher mortality in males is also illustrated in the ratio of immatures in Etosha (1 bull : 1,17 cows) which is closer to parity than the sub-adult ratio of 1 bull : 1,53 cows or the adult ratio of 1 bull : 1,57 cows. Thus there appears to be a logical progression of predation on the maturing bulls if it is considered that the sex ratio of wildebeest at birth is not significantly disparate (Braack, 1973).

Bachelor herds in Etosha were larger than those in Zululand and this would afford the individual members a greater measure of protection from predators through increased vigilance (Powell, 1974; Siegfried, 1980). The greater number of bachelor bulls present in Etosha, compared to Zululand may, in part, reflect the survival value of a larger herd size. With regard to breeding herd bulls the lower percentage of this component in Etosha can be explained by the fact that proportionately fewer

and larger breeding herds, each with a herd bull in attendance, existed in Etosha than in Zululand.

Calf survival in Etosha appeared to be higher than in Zululand (0,5 compared to 0,4; Table 6) and is confirmed by the higher percentage of calves in the total population and by the ratio of calf : adult cow.

When the mortality patterns in Etosha wildebeest are examined (Table 3) it is evident that the heaviest mortality in adults of both sexes occurred in the three- to six-year-old group (48 % of all skulls found). Furthermore, 91 % of all adult deaths had taken place at the age of 10 years. No interpretation of mortality in wildebeest younger than three years was attempted from skulls found because of the rapidity with which immature skulls and horns are destroyed. Nevertheless, the available data show that at least 14 % of population mortality occurred in the one- to three-year-old age group.

In comparison, Attwell's (1977) findings in Zululand were that 48 % of adult mortality occurred in the four- to six-year-old age group and that at 10 years of age 74 % of the adults had died. Therefore mortality in four- to six-year-old wildebeest was the same in Etosha's and Zululand's samples, but the four- to 10-year-old mortality rate was higher in Etosha (89 %). Consequently, 26 % of Zululand's adult wildebeest attained an age of more than 10 years, while in Etosha only 11 % exceeded this age.

In summary, it appeared that the mortality patterns in neo-natal calves among Etosha's wildebeest were typically high. Also, up to the age of six years mortality was very similar to declining populations in the Kruger National Park (Braack, 1973) and Zululand (Attwell, 1977). Adult mortality in Etosha was greater than other

populations, up to the age of 10 years, with only 9 % of the population surviving beyond this age. When compared to other declining populations such as in Zululand and the Kruger National Park it seems as if maximum longevity of Etosha's wildebeest is approximately 14 years and therefore about seven years less than the maximum age of 21.5 years (Braack, 1973) and 21 years (Attwell, 1977) recorded in these other populations. The data from my investigation are strongly suggestive of a normal calf mortality while the adult segment, especially lone, territorial bulls, are subjected to heavy mortality due to a combination of predators and disease. The endemic nature of anthrax in Etosha appears to have led to an unnatural predator-prey live mass ratio (Berry, 1981). This in turn has resulted in a situation where mortality exceeds the birth rate and a consequent decline in population.

4.2 The Etosha population model in comparison with other areas

The model I used simulated Etosha's wildebeest population at its annual peak in numbers, namely, the end of the calving season, which is during March. To keep parameters simple, only four age classes were used and sexes were not distinguished. Three critical parameters were selected to represent intrinsic and extrinsic pressures which may have limited the population. These are birth rate, calf survival which leads to recruitment rate, and mortality of animals older than one year. To simulate conditions in Etosha, the mortality was ascribed to the existing lion population and their yearly kill rate per adult, hunting lion. Furthermore, in doing this, I assumed that all wildebeest older than one year which died were eventually eaten by lions, although the proximate cause of death may have been disease, especially anthrax. In estimating the adult lion population and their kill rate, I referred to punch card data in the Etosha Ecological Institute from 1973-1978 and my observations during this study ($n=912$ pride compositions; $n=139$ wildebeest carcasses).

Calf survival rate was taken at 0.5 on average and simulated the mortality from the end of the calving period to one year of age which was established by observation. To simulate adult birth rate I calculated that, on average, 63 % of the adult population were cows and that they had a conception rate of 87 % (Table 2). Consequently, the upper limit for adult birth-rate would be 0.54. However, to reflect losses from aborted pregnancies, still-born calves and calf mortality at a very young age which my observations on calf survival counts did not detect, a lower value of 0.35 was used. In determining this figure, I took into account the fact that up to 50 % of new-born calves may die (Talbot and Talbot, 1963). Unlike the wildebeest population at the Kruger National Park where precociousness in two-year-olds resulted in a birth-rate of 0.21 in this age group (Starfield *et al.*, 1976), I did not record any pregnancy or calving by immature wildebeest in Etosha.

Although the seasonal rainfall influenced the wildebeest population, it tended to confound the prediction of population trend because compensatory factors may have been brought into play. For example, years of low rainfall decreased calf survival rate, but this was compensated for by a decrease in predation, because the shorter grass cover afforded wildebeest improved visibility. Conversely, in years of high rainfall the increase in calf survival was offset by improved conditions for predators. Impinging on these patterns was the considerable effect of disease, notably anthrax, which varied in intensity depending on the temporal and spatial distribution of the rainfall (Van Ness, 1971).

Consequently, anthrax outbreaks may be as severe under low rainfall conditions as when heavy rains occur (Ebedes, 1976). As a result, I have purposely "tuned" the lion population and their kill rate in the model to include the anthrax component of mortality, leaving the parameters of birth-rate and calf survival constant and based on a calculated mean.

It is clear from the model that extrinsic factors such as rainfall, predation and disease are less predictable than intrinsic properties of the population, namely birth-rate and calf survival, although birth-rate appears to be a very sensitive parameter for change in the population as will be discussed subsequently (Section 4.3).

If the Etosha wildebeest population is compared to other free-ranging populations in regard to birth-rate and calf survival, then the former parameter is somewhat lower while the latter is considerably higher than most other populations with the exception of the Wankie National Park, Rhodesia (Table 6). Etosha and Wankie have similar rainfall regimes and it may be that their aridity resulted in the apparent inability of two-year-old cows to reproduce, as well as a lower birth-rate in adult cows. However, both Etosha and Wankie had very similar calf survival rates and in both areas calves formed 22 % of the total population. Reviewing the data in Table 6 a general trend is evident, namely, that well-watered areas which support large populations of wildebeest such as East Africa appear to have higher birth-rates than the arid areas of Wankie and Etosha. In the Kruger National Park and Zululand, both areas of moderate rainfall, wildebeest birth-rates are intermediate to those in East Africa and Etosha. Conversely, the huge wildebeest herds encountered in East Africa result in a low calf survival rate, in which calf-cow separation is a major factor (Watson, 1967). The smaller herd sizes in Zululand, Wankie and Etosha appear to favour calf survival.

4.3 Sensitivity of parameters in the model to change, and future predictions

The effects of a 10 % change in each of the parameters selected for the model of Etosha's wildebeest population are clearly evident in Fig. 3. The order of increasing sensitivity to change is calf survival, lion population, lion

kill rate and wildebeest birth-rate. The parameters required for an hypothetically stable population are detailed in Table 4. It is unlikely that the population of c. 2 500 wildebeest in 1978 will remain at this level, since African ruminant populations display cyclic fluctuations (Sinclair, 1973).

The modelled changes of $\pm 10\%$ which I have applied to selected parameters could conceivably occur within the space of one seasonal year and indeed they could be much greater in the event of a natural catastrophe. It is worth noting that a 10% change in calf survival predicts an increase of 1.0% and a slightly larger decrease of 1.1% in population numbers after one year. Similarly, a 10% decrease in the lion population results in a 1.4% increase in wildebeest, while a 10% increase reduces the population by 1.9%. A decreased kill rate gives 1.6% more wildebeest, whereas an increased kill rate of the same magnitude (10%) gives 2.4% fewer wildebeest. The birth-rate is evidently the parameter most sensitive to change, namely: 3% population increase or decrease in response to a positive or negative change of 10%.

If these relatively small changes in parameters are projected to 1982 then the cumulative effect is noticeable. For example, a continued increase in calf survival of 10% results in a population increase of 5.6% and a continued 10% decrease in calf survival results in a population decrease of 5.1%. In comparison, the more sensitive parameter of birth-rate gives 8.4% increase and 7.8% decrease respectively. These predictions are for changes in single parameters only and if two or more parameters were to change simultaneously in favour or against the wildebeest population the consequences could be considerable. For instance, it is possible that prolonged drought could decrease birth-rate and calf survival and also increase adult mortality through an epidemic of anthrax (the latter effect would be reflected in the model as an increased lion kill rate).

These projections have been made with the view to underlining the sensitivity of the Etosha wildebeest population to relatively small changes in their environment. The consequences of a drastically altered environment in other wildebeest habitats, notably the Kruger National Park, are evident in the findings of Shiell and Starfield (1977) that wildebeest are not as resilient to change as, for example, Burchell's zebra. It follows that any attempt to modify a particular parameter in Etosha, for instance by culling lion, may allow the wildebeest population to recover, but could very well lead to an explosion of the zebra population. Management plans should as a result be made with circumspection, since the model proposed here has been purposely simplified, thereby isolating the wildebeest population from the remaining ecosystem to a great extent. Nevertheless, the model I have presented serves as a first approximation by applying available data. It can be used, albeit cautiously, as a baseline to predict what would happen to the wildebeest population in a particular situation.

5 SUMMARY

Following an apparent drastic decline in the wildebeest population in Etosha from c. 25 000 to 3 000 over a period of 20 years, a series of total counts were made by aircraft to establish the population size more accurately. During the five-year study period the numbers decreased by a further 24% (3 300 to 2 500).

Age-sex ratios were established by seasonal observations over a period of three years. Calf percentage was normal in comparison to other areas in Africa, but lone, territorial bulls were proportionately fewer than another declining population in Zululand. However, because of relatively large bachelor herds, total percentage of bulls in the population did not differ greatly from other areas. The size of Etosha's breeding herds was, on average, 34 animals compared to 14 animals in the Zululand population. Consequently, proportionately fewer herd bulls were present in Etosha. Maturing wildebeest reflected a disproportionate, sex-linked mortality favouring the cows, the adult ratio being 1 bull : 1.57 cows which was closer to parity than sex ratios in the Kruger National Park, but more disparate than in Zululand.

From a sample of 283 collected skulls, mortality patterns were related to age by tooth attrition and to sex ratios by horn development. Immature animals were under-represented in the sample, invalidating the use of skulls as a means of gauging immature mortalities. Adult mortality in both sexes was greatest between three and six years of age (48% of all skulls found) and by 10 years of age 91% of all adults had died. The maximum longevity recorded was approximately 14 years. These mortality patterns correspond well with those found in two other declining populations except that fewer wildebeest in Etosha survived beyond 10 years and maximum longevity was reduced by about seven years. A combination of diseases (anthrax) and predation pressure appeared to be the most likely cause of this early adult mortality.

A computer model was used to simulate the declining population by manipulating the critical parameters of birth-rate, calf survival and combined mortality in all other age groups. Plausible mean values were 0.35 for birth-rate which took into account neo-natal deaths and 0.5 for calf survival. Mortality rates in animals older than one year were established from field observations and gave a yearly range of 260–700 during the five-year period on which the population was modelled. This mortality exceeded the recruitment rate of two-year-old wildebeest to the breeding stock. Lions were assumed to be the ultimate factor in wildebeest mortality for the purpose of the model although anthrax disease was in many instances the proximate factor. Birth-rate was found to be the population parameter which was the most sensitive to change, followed by lion kill rate, the number of lions and lastly calf survival rate. Furthermore, overall birth-rate in Etosha wildebeest appeared to be lower than most other free-ranging populations, partly because cows in their second year did not reproduce.

This lower birth-rate appeared to be compensated to a certain extent by a normal to above average calf survival rate.

Projections of population trends until 1982 showed that relatively small changes in the parameters, namely a 10% increase or decrease, would result in changes of between 5 and 9% in total population. However, in the event of a succession of major, unfavourable changes in the environment, such as could be expected under drought conditions, the wildebeest population would decline drastically. The model was a gross simplification of the complicated ecological processes governing the wildebeest population and did not consider the species interactions which would be effected in the event of changed parameters.

When viewed against the past history of Etosha, where changed conditions have resulted in the present drastically reduced wildebeest population, it seems unlikely that the former numbers will be regained. Instead, management plans should be directed at maintaining the wildebeest population at its present level. Since disease, notably anthrax, appeared to be the proximate cause of decline during the study, further research in this field is essential. The culling of lion or other predators is not recommended because it may only serve to alleviate the symptoms. The obvious choice is to treat the cause, not the effect.

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