BEHAVIOURAL AND ECO-PHYSIOLOGICAL STUDIES
on
BLUE WILDEBEEST (*Connochaetes taurinus*)
at the
ETOSHA NATIONAL PARK

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VOLUME II

TABLE OF CONTENTS

Page No.

VOLUME I

Page No.

VOLUME II

Page No.

VOLUME II

Section 8

NUTRITIONAL BALANCE : GRASSLAND PRODUCTIVITY VERSUS HERBIVORE DEMAND

8.1 INTRODUCTION

Interspecific competition for food resources needs to be examined when determining which factors are regulating a population of wild ruminants (Sinclair, 1974, 1977). My assumption was that competition existed between the wild herbivores sharing the open grassveld at Etosha. However it was also possible that mutualism occurred within this larger concept, for example when zebra opened up areas of tall grass to wildebeest, which grazed at a lower level (Bell, 1969, 1971). Nevertheless, potentially competitive species have been confined within Etosha's boundaries since 1973. During this relatively short period of five years, the long term adaptations which tend to minimise direct interspecific competition (Moen, 1973), have not had sufficient time to develop. Consequently, the present interspecific grazing association may very well be unstable, favouring those herbivores which are catholic in their foraging habits. Less flexible feeders, such as wildebeest (Watson, 1967; Attwell, 1977), could suffer under these conditions. Furthermore, competition may have been linked to the seasons, for example when the food resources or a specific nutrient became limiting during dry season dormancy.

In this Section I will estimate energy and protein requirements in the major competitors of wildebeest at Etosha, taking into account their age-sex ratios and population trends. Thereafter, I intend balancing the energy-protein supply of the grasslands against the seasonal demand for these critical nutrients by the large herbivores, including wildebeest. This approach will make it possible to establish whether competition for food existed and if so, which seasons and areas were involved.

The five major herbivore species which, together with wildebeest, inhabited the open grassland of Etosha were Burchell's zebra, springbok, gemsbok, red hartebeest and ostrich. All are large in size and were relatively easy to observe from the ground, although springbok were often overlooked during aerial censuses. The red hartebeest, by preference a bush and woodland dweller at Etosha, was not uncommon on the plains. Consequently, I have included this species with the food competitors of wildebeest by referring only to the numbers counted on the plains. No attempt was made to assess the status of smaller herbivores which inhabited the plains, such as ground squirrels and hares. Neither were graminivorous birds taken into account.

8.2 METHODS

8.2.1 Aerial Counts

Estimates of the numbers of major competitors were made during aerial census of wildebeest (Section 12). I carried out four major censuses of competitors by helicopter from 1974 - 1978 and referred to earlier counts by Ebedes *et al.* (1970) and Joubert *et al.* (1973). Only two age classes could be distinguished during aerial counts, namely animals less than one year old and those older than one year. Competitors could not be sexed during these observations.

8.2.2 Ground observations

More detailed age-sex classes were established during observations made from a vehicle, over a period of four years (1974 - 1978). All five major competitors were sexed and divided into three age classes : less than one year old, one to two years old, and full grown. To avoid bias in determining the populations' structure, family units or whole herds were aged and sexed when possible.

8.2.3 Calculation of Energy Budgets

In the absence of quantitative data on activity patterns and related energy budgets in the ruminant competitors of wildebeest at Etosha, I applied the increments over RMR which had been established for the various age-sex classes of wildebeest (Section 5.3.7.5) to the competitors. These theoretical values probably approximate those which exist in other ruminants, namely springbok, gemsbok and red hartebeest, since ruminants have basically similar needs for free existence (Moen, 1973). In the case of free-living zebra, increment over RMR is also unknown, but may be somewhat lower than that of ruminants because zebra may be able to utilise more fibrous grasses (Janis, 1976). Consequently, zebra may be less active than the selectively foraging wildebeest. I have nevertheless allocated an arbitrary mean value of 2,0 for increment over RMR in zebra. This is based on the minimum value of 1,5 for activity alone and an upper limit of 2,3 when the energy demands of growth, gestation and lactation are considered (Moen, 1973). Similarly, because increment over RMR in free-living ostrich is unknown, an arbitrary value of 1,9 was allocated, which made allowance for the fact that gestation and lactation were not involved (refer Section 5.3). Nevertheless, an energy cost for egg production does exist, and was added to the increment over RMR of 1,9 in adult hens. Similarly, the energy cost of incubation to both cocks and hens was considered (Siegfried and Frost, 1974) and added to the increment over RMR of 1,9 in both adult sexes.

To estimate the energy cost of egg production in ostrich, I used a mean fresh egg mass of 1 187 g (Sauer and Sauer, 1966) and, based on the mean mass of 10 ostrich egg shells which I found to be 19 % of the total egg mass, I calculated the yolk and albumen to be 962 g per egg. Assuming that 13 % of the yolk and albumen is composed of protein and 10,5 % is fat (Maynard and Loosli, 1962), the protein content of an egg was taken to be 125 g and the fat content 101 g. Applying Durnin and Passmore's (1967) calorific values of 5,4 for protein and 9,12 for fat, I estimated that one egg would contain 1 596 kcal. Furthermore, based on data for domestic animals (Crampton and Harris, 1969), I assumed that the total energetic cost of egg production was 1,6 times the energy contained in the egg. The energy cost of one ostrich egg was estimated at 2 554 kcal (10 684 kJ). Taking the average annual production of an ostrich hen at eight eggs (Sauer and Sauer, 1966), the energy cost to a laying hen would be 85 472 kJ.year^{-1}. Because the rate of successful egg production in wild ostrich is unknown, I assumed that 90 % of the adult hens would lay a full clutch every year.

The additional energy cost of incubation was based on data from Siegfried and Frost (1974), namely 165,2 kcal/bird-day for ostrich cocks and 116,6 kcal/bird-day for hens. Incubation was taken at 42 days (Sauer and Sauer, 1966; Siegfried and Frost, 1974). Thus the total annual cost of incubation was estimated to be 6 938 kcal (29 030 kJ) for cocks and 4 897 kcal (20 490 kJ) for hens, 90 % of which were presumed to breed each year.

The basic calculation of RMR was 70 $W_{kg}^{0,75}$kcal.day^{-1} (National Research Council, 1966) for all mammalian competitors. For RMR in ostrich I applied Lasiewski and Dawson's (1967) regression equation for non-passerine birds of 78,3 $W_{kg}^{0,723}$kcal.day^{-1}.

8.2.4 Calculation of Protein Budgets

Nitrogen requirements for maintenance, growth, gestation and lactation were calculated for the major competitors, using the equations detailed in Section 6. In the case of ostrich, I estimated nitrogen requirements for egg production. Subsequently, protein budgets were derived for individuals and the populations as described in Sections 6.3.5 and 6.3.7. I now propose to deal briefly with the method of computing nitrogen requirements for each of the five species of competitor.

8.2.4.1 Zebra

The basic formulae for calculating nitrogen requirements in wildebeest were applied to zebra (Moen, 1973; cf. Section 6.2). For data on mean body mass, growth and gestation in zebra I referred to the substantial findings of Smuts (1974). Furthermore, when calculating MFN, the seasonally changing milk : forage ratios of foals were taken into account. In the calculation of Q_{ng}, the RN (retained nitrogen) values were taken at 3,5 % for zebra foals and 2,4 % for the one to two year old class (Section 6.2.1.2). The expression of Q_{nh} used for zebra included a correction factor of 0,6 to allow for the relatively short pelage. Q_{np} in zebra takes into account the duration of pregnancy, which is ± 375 days (Smuts, 1974). The calculated value of Q_{np} was 29,63 $g.day^{-1}.kg$ foetus mass at term, which gave a total cost of 1 007,42 g N per pregnancy (29,63 x 34,0 kg birth mass). Q_{nl} was computed by allocating a value of 0,48 % nitrogen in the milk, derived from a protein content of 3,0 in the milk of *Equus* spp. (A. Smith, 1970). The quantity of protein required by a zebra foal was taken at 3,3 $g.day^{-1}$, which is the lower figure in the range of 3,3 - 6,6 given by Moen (1973). All other components of the expression for estimating Q_{nl} were the same as for wildebeest (Section 6.2.1.4).

8.2.4.2 Springbok

Biometric data required for the estimation of nitrogen demand in springbok were obtained from Dorst and Dandelot (1970), Mentis (1972) and Appendix 26. The expressions used were based on those for ruminants (Moen, 1973) and followed the computations applied in the case of wildebeest (Section 6.2), except where obvious differences in species occur. For instance, the relatively short gestation period of ± 170 days in springbok (Mentis, 1972) necessitated a change in the constants used in the expression Q_{np} (Section 6.2.1.3). Consequently, I applied the data for domestic sheep as a baseline, where foetal mass at term is 5,9 kg and gestation runs to 140 days (Moen, 1973). Thereby the equation fitted to the expression of Q_{np} in the case of springbok was

$$e^{(-2,3623 + 0,0407)}$$

assuming that a single lamb is born (Moen, 1973). Furthermore, only the dry, hot season is involved to any appreciable extent in the nitrogen demand for gestation in springbok. Another instance of difference in nitrogen requirement of springbok when compared to wildebeest is the length of the pelage, which is greater in springbok, especially on the rump. Accordingly, in the expression of Q_{nh}, I applied an arbitrary conversion factor of 0,8 instead of 0,6 (Section 6.2.1.2). Springbok milk has a protein content of 8,0 % (A. Smith, 1970). Thus, to calculate Q_{nl}, the nitrogen present in the milk was taken at 1,28 %.

8.2.4.3 Gemsbok

Gemsbok are similar in body mass (Tables 5.1 and Appendix 26 of this thesis) and gestation period (264 days; Mentis, 1972) to wildebeest. Consequently their nitrogen requirements will be comparable. For additional biometric data on gemsbok I referred to Ebedes (1969) and Dorst and Dandelot (1970). All equations used for the estimation of nitrogen demand in gemsbok were based on those applied to wildebeest (Section 6.2).

8.2.4.4 Red Hartebeest

Red hartebeest require much the same intake of nitrogen as wildebeest to meet the demands of free existence. However, the body mass of hartebeest is lower (Dorst and Dandelot, 1970 and Appendix 26). Also their gestation period is shorter (242 days, Mentis, 1972) and calving is usually completed by August. This resulted in a proportionately lower daily demand and no Q_{np} (gestation) value during the dry, hot season (Appendix 32). As in the case of gemsbok, I based the calculation of nitrogen requirements for red hartebeest on those used for wildebeest (Section 6.2).

8.2.4.5 Ostrich

Because ostrich may breed in all seasons at Etosha with a peak in the dry, cold season (personal observations), I allocated similar seasonal nitrogen requirements to the various age-sex classes throughout the year. Furthermore, EUN in ostrich is better estimated by taking into account their RMR, which differs from mammals (Lasiewski and Dawson, 1967).

$$\text{Thus} \quad Q_{eun} = \frac{2 \times 78{,}3\ (W_{kg}^{0{,}723})}{1000} \quad \text{(cf. Section 6.2.1.1)}$$

Q_{mfn} in ostrich was calculated by taking a value of 5,0 g DM.kg^{-1}.day^{-1} (ARC, 1965) for all age classes, since a liquid diet in the form of milk plays no part. Q_{nh} was considered to represent the nitrogen requirement for feather growth and replacement. With no published data available on this requirement in ostrich, an arbitrary correction factor of 2,0 times that required for hair production in mammals was applied. Obviously, Q_{np} and Q_{nl} cannot be considered for ostrich, although nitrogen is needed for egg production. To calculate nitrogen demand in laying hens, I assumed that 125 g protein occurred, on average, in an ostrich egg (Section 8.2.3). Consequently there would be 20 g N x 8 eggs = 160 g N required per egg clutch. To obtain the total cost of nitrogen required to produce the eggs, I multiplied 160 g N by a factor of 1,38 (Crampton and Harris, 1969), thereby obtaining a final estimate of 221 g N.year^{-1} per laying hen. Finally, 90 % of the adult hens were presumed to lay each year.

8.3 RESULTS

8.3.1 Population Estimates and Trends

Counts of the major competitors of wildebeest over an

11-year period (1968 - 1978) were available from reports of previous workers at Etosha and my observations. These are given in Appendix 25 together with the corrected values which were calculated. A summary is presented in Table 8.1. The limitations imposed by the type of aircraft available have been discussed in Section 12.

Aerial counts are underestimates of the total population of a wild animal species (Melton, 1978a). Furthermore, most species give such variability in successive counts that aerial censuses may be invalid even as an indicator of trend in population (Melton, 1978b). It is therefore not surprising that the results in Table 8.1 are characterised by great variability. The findings at Etosha support those of Melton (1978a, b), namely that wildebeest (Section 12) and zebra are reliable species in aerial counting because the bias factor for undercounting is relatively small and they can consequently be used as indicators of population trends. However, the margin of error by which springbok, gemsbok, red hartebeest and ostrich are undercounted has not been determined. Springbok especially, are difficult to see from an aircraft under certain conditions and so the counts made on them as well as the remaining competitors must be treated with caution. Moreover, the tendency to undercount is clearly demonstrated in Appendix 25 by the

Table 8.1 : Corrected aerial counts of the five major competitors of wildebeest at Etosha (1968 - 78)

Year*	Method	Species				
		Burchell's Zebra	Springbok	Gemsbok	Red Hartebeest	Ostrich
1968	Fixed-Wing Aircraft (Fwa)	18 073	3 364	1 902	124	316
1969	Fwa	22 284	15 351	3 692	95	1 437
1970	Fwa	14 110	9 892	2 509	88	2 784
1972	Fwa	16 426	7 025	2 726	110	786
1973	Fwa	10 244	7 493	1 131	95	603
1973	Fwa	15 053	10 517	2 764	138	1 802
1973	Helicopter (H)	13 902	8 367	2 201	128	822
1974	H	16 002	9 800	2 081	167	707
1976	H	11 035	16 411	902	103	667
1977	H	9 414	31 493	1 247	73	1 222
1978	H	9 166	32 076	642	128	724
	Mean	14 155	13 799	1 982	114	1 079
	± SD	±4 041	±9 604	± 930	±27	± 705

*1968-70 from Ebedes *et al.* (1970)
1972-73 from Joubert *et al.* (1973)
1974-78 present study.

overall lower figures obtained with the fixed-wing aircraft, which had greater limitations in regard to visibility, speed and manoeuvreability than the helicopter.

In addition, the five competitors were not exclusively limited to the open plains, but moved back and forth to the woodland areas of Etosha for varying lengths of time. This may also explain the peaks and troughs in successive years' counting, since aerial surveys concentrated on the plains. Wildebeest, in contrast, were almost exclusively encountered on the treeless grasslands of Etosha.

I propose to approach these problems by firstly considering the overall numerical trend in each competitive species and secondly, by making an adjustment to the actual numbers counted, which may compensate for undercounting bias. For the purpose of this study, the numbers of competitors can only be applied meaningfully from 1973 onwards, since this is the first year in which yield data of the grasslands were available.

8.3.1.1 Zebra

Reviewing their three aerial surveys (1968-1970), Ebedes *et al.* (1970) were of the opinion that the zebra population did not exceed 15 000 and was probably decreasing.

Furthermore, between 1974 and 1978 a decline in the population became evident. The helicopter counts suggested this, and they were substantiated by ground counts which showed a low recruitment rate. To correct for undercounting bias, a factor of 1,22 was applied to each helicopter count, since Melton (1978a) found that, on average, 82 % of zebra were seen from the air. Moreover, allowance was made for the number of zebra counted in the western area of Etosha. They are a discrete sub-population which do not cross the ecological barrier imposed by an 80 km wide area of mopane shrub. To obtain comparable figures between the types of aircraft used, it was necessary to allow for a greater margin of undercounting bias by fixed-wing aircraft. In the case of zebra this was 37 % lower than the helicopter counts and so the adjustment factor was 1,59. Thereafter, the factor for helicopter undercounting (1,22) was applied to estimate the actual number of zebra present.

8.3.1.2 Springbok

In contrast to zebra, the springbok population appeared to have increased very significantly in the past decade. Helicopter counts showed a doubling in number during 1976-1977. This was probably due to a mass movement from the bush and woodland areas onto the plains, which augmented the natural rate of increase. Ebedes *et al.* (1970) were unwilling to state a figure for the population because they regarded their springbok counts as inaccurate. I used a correction factor of 1,40 to allow for undercounting between fixed-wing aircraft and helicopter (Joubert *et al.*, 1973), and a factor of 1,69 for undercounting by helicopter. In the latter case springbok were considered equal to impala, of which 59 % were counted from a helicopter under favourable conditions (Melton, 1978a). As with zebra, springbok found to be ecologically separated from the wildebeest population were not included in the calculations.

8.3.1.3 Gemsbok

The population was considered to be relatively stable. Fixed-wing aircraft counts were, on average, 77 % of the total counted by helicopter. Consequently a factor of 1,30 was used to make them comparable with the helicopter counts. In the absence of data on undercounting bias of gemsbok by helicopter, a correction factor of 1,22, based on zebra (Melton, 1978a), was used. Only gemsbok sighted on or near wildebeest habitat were included in the corrected counts.

8.3.1.4 Red Hartebeest

This species cannot be considered a true plains animal at Etosha and only those found in or near areas of wildebeest habitat were included as food competitors. To compensate for undercounting bias, a fixed-wing aircraft : helicopter ratio of 1,02 (Joubert *et al.*, 1973) was used. The factor for undercounting by helicopter was 1,69 which is the same as for springbok and was based on the visibility of impala to the observer in a helicopter (Melton, 1978a).

8.3.1.5 Ostrich

Their distinctive plumage made cocks easily visible from the air, but hens and immatures were difficult to see. Considering this, a correction factor of 1,46 for undercounting by helicopter was applied. This is the intermediate value between zebra (1,22) and impala (1,69) when counted under favourable conditions (Melton, 1978a). According to Joubert *et al.* (1973), 87 % of the ostrich sighted by helicopter were seen from a fixed-wing aircraft, giving a conversion factor of 1,15.

8.3.2 Age-Sex Ratios

In the course of five years (1974 - 78), I aged and sexed the major competitors of wildebeest from a vehicle and a hide. The majority of these observations were made at waterholes where animals usually approached in file to drink. In total, 13 191 animals were aged visually, of which 2 999 (23 %) could be accurately sexed. The results are given in Table 8.2.

8.3.2.1 Zebra

The three age classes were determined subjectively. Because growth data indicate that visual age classification of zebra in the field is only reliable up to the age of about two years (Smuts, 1974), I placed all full-grown zebra into a single age category. There may have been some error in the ageing of yearlings which were difficult to distinguish in size from the animals entering the one to two-year old class. Nevertheless, the results were consistent with those of Kruger Park zebra, where 11,95 % were under one year of age, 6,28 % were one to two years old, and 81,78 % were fully grown (Smuts, 1974). Sexing of zebra was done by observing differences in the shape of the perineal skin (Smuts, 1974) and by the extrusion of the penis, which is a common feature of zebra stallions at Etosha. Sex ratios of Etosha's zebras were similar to Kruger Park, where 44 % of the sub-adults and adults (two years and older) were stallions and 56 % were mares (Smuts,

Table 8.2 : Age-sex ratios of the five major competitors of wildebeest at Etosha (1974 - 78)

Species	Age				Sex		
	No. of observations & % of population	Full grown	1-2 yrs	< 1 yr	No. of observations & % of population	Male	Female
Burchell's zebra	6 680	5 417,0	545,0	718,0	559	262,0	297,0
	%	81,1	8,1	10,8	%	46,9	53,1
Springbok	4 101	2 830,0	324,0	947,0	1 475	585,0	890,0
	%	69,0	7,9	23,1	%	39,7	60,3
Gemsbok	936	780,0	83,0	73,0	215	57,0	158,0
	%	83,3	8,9	7,8	%	26,5	73,5
Red hartebeest	532	422,0	44,0	66,0	241	112,0	129,0
	%	79,3	8,3	12,4	%	46,5	53,5
Ostrich	942	766,0	151,0	25,0	509	258,0	251,0
	%	81,3	16,0	2,7	%	50,7	49,3

1974). The Etosha ratio of 1 stallion : 1,13 mares deviated significantly from parity ($X^2 = 4,12$ at $P < 0,05$). This is a well established phenomenon in most large African herbivores, namely that mortality rates are higher in adult males (Mentis, 1972).

8.3.2.2 Springbok

The stages of horn growth in both sexes made it relatively easy to place springbok in the three broad age categories used here. Age distribution in the sample taken suggested an expanding population (Odum, 1971) and was confirmed by the aerial counts (Table 8.1). Etosha's population was comparable to the population composition of springbok in the Bontebok National Park (David, 1978a) where 63 % were adult and 37 % were juvenile. Furthermore, the sex ratio of springbok at Etosha was 1 ram : 1,50 ewes which was disparate ($X^2 = 104,52$ at $P < 0,001$). Earlier studies at Etosha and Kalahari Parks gave ratios of 1 ram : 1,75 - 2,33 ewes, which were even further from parity (Bigalke, 1970).

8.3.2.3 Gemsbok

No intensive studies have been completed of the population structure and sex ratios of gemsbok (Estes, 1974).

Consequently, I used earlier observations from Etosha for comparison with my data. Du Preez (1971) found that 85 % of the population were adults, 9 % were yearlings, and 6 % were calves. This parallels my findings in the present study. An interesting aspect of both these sets of data was that yearlings appeared to be more numerous than calves. However, this was probably due to the cryptic colouring and the concealment behaviour in young gemsbok calves which is characteristic of the "Ablieger Typ" or "hiders" (Estes, 1974; Walther, 1978, pers.comm.). Insofar as sex ratio was concerned, records kept since 1971 on a punch card system at Etosha gave 1 bull : 2,28 cows (n = 439) which is remarkably similar to my findings of 1 bull : 2,77 cows. Both sets of data are disparate (X^2 = 95,87 and 64,56 respectively, at $P < 0{,}001$). In a relatively small sample (n = 97) from Kalahari Park, there were 23 bulls and 74 cows (Mentis, 1972). This is a ratio of 1 bull : 3,22 cows and supports my data, being disparate (X^2 = 35,15 at $P < 0{,}001$).

8.3.2.4 Red Hartebeest

Very little is known about the social organisation and population structure of red hartebeest and only cursory reference has been made to the species in this respect (i.e., Estes, 1974). However, Mentis (1972) presented a brief demographic picture of sex ratios. Comparison of my data was limited to his summary and to observations carried out at Etosha by earlier workers. Joubert *et al.* (1973) found from aerial counts that calves comprised 16 % of the population. My observations from a helicopter gave a calf component of 8 % - 16 % and so the figures of 12,4 % (calves) and 8,3 % (one to two-year olds) that I obtained by ground counts, seemed reasonable. However, in regard to sex ratio my data were at complete variance with those reflected in the punch cards of nature conservators at Etosha since 1971. They recorded a ratio of 1 bull : 1,82 cows (n = 843) which was disparate (X^2 = 110,34 at $P < 0{,}001$), whilst my figures favoured females only slightly (1 bull : 1,15 cows) and did not differ significantly from parity (X^2 = 2,24 at $P > 0{,}10$). Also, my findings agreed closely with the review published by Mentis (1972) which gives a ratio of 1 bull : 1,01 cows, being virtually at par (X^2 = 0,04 at $P > 0{,}80$).

8.3.2.5 Ostrich

There appear to be no reliable data on age-sex ratios in wild populations of ostrich, although Sauer and Sauer (1966) regarded a ratio of 1 cock : 3 hens to represent a "balanced" population in sexually mature ostrich at Etosha and in the Namib Desert. Records from punch cards kept at Etosha since 1971 gave a ratio of 1 cock : 1,07 hens (n = 313) which is at parity (X^2 = 0,75 at P > 0,30). This was confirmed by my observations of 1 cock : 0,97 hens (X^2 = 0,20 at P > 0,50). Furthermore, ostrich are normally monogamous (McLachlan and Liversidge, 1978) and so my findings at Etosha appeared acceptable. It should be noted however, that aerial census of ostrich have given unreliable figures in which the sex ratio appears significantly disparate, favouring the cocks. This is because cocks are more easily visible than hens from an aircraft. For example, Joubert *et al.* (1973) found a ratio of 1 cock : 0,9 hens (n = 479) and I have recorded ratios of 1 cock : 0,4 - 0,7 - 0,8 - 0,9 hens during four counts by helicopter.

The small number of chicks observed (2,7 %) in relation to the total sample was probably due to the fact that young birds and their parents were not seen at waterholes, where most of my observations on age-sex ratios were made. This would be a logical defence mechanism against predators. All chicks seen were found away from waterholes, in vegetation which favoured their cryptic colouring, and this biased the observations further. Consequently, the number of one to two-year old birds (16 %) appeared disproportionately high. Nevertheless, chick mortality may be very high, as I have frequently seen a pair of ostriches with less than five chicks, whilst 15 - 20 eggs may be laid (McLachlan and Liversidge, 1978).

8.3.3 Energetic Cost of Free Existence

Energy budgets for the five major competitors of wildebeest were calculated for the individual animal on a daily and yearly basis (Appendix 26) and summarised in Table 8.3. Thereafter, the population energy budgets for all herbivore species were approximated on a yearly basis for the period 1973 - 78. This was achieved by applying the relevant census figures for each year. When calculating energy demands for seasons other than 1977/78, my assumption was that the increments over RMR remain the same. The reason for this is that activity budget details strictly apply only to 1977/78 (Section 4) and the calculations involved for estimating all the parameters for free existence would be too time consuming in terms of the small benefit in increased accuracy. Nevertheless, I attempted to set up as many age-sex classes as possible, with their accompanying means in body mass, to calculate $70W_{kg}^{0,75}$ and $78,3W_{kg}^{0,723}$. I then applied the number of individuals in each class, rather than taking mean biomass of whole populations. These yearly energy budgets are presented in Appendices 27 to 31 and summarised in Table 8.4.

Table 8.3 : Yearly, individual energy budgets for five major competitors of wildebeest at Etosha

Species	Age-Sex Class	Energy Requirements ($MJ.year^{-1}$)
Burchell's Zebra	0 - 1 year	9 528
	1 - 2 years	12 833
	Full-grown female	16 742
	Full-grown male	16 100
Springbok	0 - 1 year	2 335
	1 - 2 years	2 878
	Full-grown female	3 063
	Full-grown male	2 751
Gemsbok	0 - 1 year	5 653
	1 - 2 years	9 137
	Full-grown female	11 664
	Full-grown male	10 169
Red Hartebeest	0 - 1 year	4 643
	1 - 2 years	7 884
	Full-grown female	9 186
	Full-grown male	8 195
Ostrich*	0 - 2 years	4 385
	Full-grown female	7 019
	Full-grown male	7 238

* The energetic cost of egg production and incubation was added when calculating the population energy budget (Table 8.4).

Table 8.4 : Estimated yearly population energy budgets for the five major competitors of wildebeest at Etosha (1973 - 1978)

Species	Year	Total Energy Requirements ($terajoules.year^{-1}$)
Burchell's Zebra	1973	214,1
	1974	246,2
	1975	208,2
	1976	170,0
	1977	145,0
	1978	141,2
Springbok	1973	23,4
	1974	27,4
	1975	36,6
	1976	45,9
	1977	87,8
	1978	89,7
Gemsbok	1973	23,1
	1974	22,1
	1975	15,9
	1976	9,6
	1977	13,3
	1978	6,8
Red Hartebeest	1973	1,0
	1974	1,4
	1975	1,1
	1976	0,8
	1977	0,6
	1978	1,0

Table 8.4 (continued)

Species	Year	Total Energy Requirements (terajoules.year^{-1})
Ostrich	1973	5,5
	1974	5,1
	1975	4,9
	1976	4,8
	1977	8,7
	1978	5,2

In the case of ostrich, I added the energetic cost of egg production and incubation to the increment over RMR, which was 1,9. For example, in 1973 the ostrich population was estimated to be 822 (Appendix 31), of which 81,3 % (668) were adult (Table 8.2). Furthermore, 49,3 % (329) of the adults were hens and 50,7 % (339) were cocks (Table 8.2). Assuming that 90 % (296) of all adult hens laid a complete clutch, then 296 x 85 472 $kJ.year^{-1}$ (Section 8.2.3) = 25 299 712 $kJ.year^{-1}$ would be required for egg production. To calculate the energetic cost of incubation for 1973, I assumed that one hen in three, namely 99 hens, would incubate (Sauer and Sauer, 1966). Therefore 99 x 20 490 $kJ.year^{-1}$ (Section 8.2.3) = 2 028 510 $kJ.year^{-1}$ would be required for incubation by hens. Similarly, 2 873 970 $kJ.year^{-1}$ would be required by incubating cocks.

No aerial census was undertaken in 1975 and so I applied the mean of the population numbers in 1974 and 1976 to all species of competitors. In 1973 when three aerial censuses were made (Table 8.1), I used the helicopter census for my estimates of population energy budgets because the subsequent censuses were also done by helicopter.

8.3.4 Nitrogen Demand for Free Existence

The nitrogen demand in free-living wildebeest has been discussed on a seasonal basis in Section 6. A similar estimation of the individual, daily nitrogen requirements in competitors of wildebeest is presented in Appendix 32 and summarised in Table 8.5.

8.3.5 Protein Budgets

Seasonal protein budgets were first calculated for individual animal competitors (Table 8.6) by applying a conversion factor of 6,25 to the daily nitrogen demand (Table 8.5) to obtain the amount of protein required (ARC, 1965). Thereafter the seasonal protein budgets for populations of competitors could be computed for the period 1973 - 78 (Appendices 33 to 37) and are summarised in Table 8.7. For this purpose the estimated populations in each year (Table 8.1) were taken in conjunction with the age-sex ratios which had been obtained (Table 8.2).

8.4 DISCUSSION

8.4.1 Energy Supply and Demand

The energy demand of the wildebeest population was based on that estimated for 1977 - 78 (Section 5) and the

Table 8.5 : Estimated seasonal, individual nitrogen budgets for five major competitors of wildebeest at Etosha

Species	Age-sex class	Seasonal nitrogen requirements $(g.day^{-1})$		
		Wet, hot season (Jan. to April)	Dry, cold season (May to Aug.)	Dry, hot season (Sept. to Dec.)
Burchell's zebra	0-1 yr	13,38	19,13	22,41
	1-2 yrs	17,86	17,15	18,14
	Full-grown female	80,56	85,27	63,90
	FG male	19,07	16,53	16,53
Springbok	0-1 yr	3,13	3,79	4,64
	1-2 yrs	3,40	3,49	3,70
	FG female	11,86	8,56	3,34
	FG male	3,64	3,32	3,32
Gemsbok	0-1 yr	10,68	12,30	13,87
	1-2 yrs	13,08	13,04	14,76
	FG female	44,53	23,11	30,83
	FG male	15,05	13,30	13,30
Red hartebeest	0-1 yr	8,33	9,53	10,83
	1-2 yrs	10,84	11,01	12,06
	FG female	34,68	16,26	30,88
	FG male	11,75	10,29	10,29
Ostrich*	0-2 yrs	9,43	9,91	9,91
	FG female	8,84	7,92	7,92
	FG male	9,14	8,18	8,18

* The nitrogen cost of egg production was added when calculating the population protein budget (Table 8.7).

Table 8.6 : Estimated seasonal protein budgets in individual competitors of wildebeest at Etosha

Species	Age-sex class	Individual protein requirements (kg DM)		
		Wet, hot season (Jan. to April)	Dry, cold season (May to Aug.)	Dry hot season (Sept. to Dec.)
Burchell's zebra	0-1 yr	10,035	14,706	17,088
	1-2 yrs	13,395	13,184	13,832
	Full-grown female	60,420	65,551	48,724
	FG male	14,303	12,707	12,604
Springbok	0-1 yr	2,348	2,913	3,538
	1-2 yrs	2,550	2,683	2,821
	FG female	8,893	6,581	2,547
	FG male	2,730	2,552	2,532
Gemsbok	0-1 yr	8,010	9,456	10,576
	1-2 yrs	9,810	10,025	11,255
	FG female	33,398	17,766	23,508
	FG male	11,288	10,224	10,141
Red hartebeest	0-1 yr	6,248	7,326	8,258
	1-2 yrs	8,130	8,464	9,196
	FG female	26,010	12,500	23,456
	FG male	8,813	7,910	7,846
Ostrich[x]	0-2 yrs	7,073	7,618	7,556
	FG female	6,630	6,089	6,039
	FG male	6,855	6,288	6,273

[x] The protein cost of egg production was added when calculating the population protein budget (Table 8.7).

Table 8.7 : Estimated yearly population protein budgets for the five major competitors of wildebeest at Etosha (1973 - 78)

Species	Year	Total Protein Requirements (Metric tons DM)
Burchell's Zebra	1973	1 363
	1974	1 570
	1975	1 326
	1976	1 072
	1977	923
	1978	897
Springbok	1973	103
	1974	121
	1975	161
	1976	202
	1977	387
	1978	401
Gemsbok	1973	127
	1974	120
	1975	86
	1976	52
	1977	71
	1978	37
Red Hartebeest	1973	5
	1974	7
	1975	5
	1976	4
	1977	3
	1978	5

Table 8.7 (continued)

Species	Year	Total Protein Requirements (Metric tons DM)
Ostrich	1973	17
	1974	14
	1975	14
	1976	13
	1977	25
	1978	15

additional estimates for the period 1973 - 78 are given in Table 8.8. The combined supply and demand for energy by wildebeest plus their major competitors is set out in Table 8.9. These data are based on the supply and balance of energy as measured in Section 7 and the theoretical demand and resultant balance calculated in Section 8.3.3 From the results obtained in Table 8.9, it appeared that I consistently underestimated demand for the five years for which reliable data were available. Furthermore, from the rainfall recorded, it was evident that this underestimation occurred during years of low, average and high rainfall. The mean rainfall for the period 1973 - 78 (476 mm) was, however, above the norm of 419 mm for the study area. Thus my investigation took place during a wet cycle.

I will now discuss the possible errors in my estimates which indicate that I employed a conservative method for calculating energy demand. Firstly, the energetic cost of rumination could not be estimated during the study on activity patterns of wildebeest (Section 4). Likewise, I only examined the lower critical temperature range encountered by wildebeest (Section 5). I also did not consider the energy drain by parasites which, although it may be negligible in the case of wildebeest, would almost certainly be a considerable factor in zebra at Etosha,

Table 8.8 : Estimated yearly energy budgets for the wildebeest population on the grasslands of Etosha (1973 - 1978)

Year	Estimated Population	Total Energy Requirements ($kJ.year^{-1}$)
1973	3 717	36 532 525 259
1974	3 300	32 434 233 426
1975	2 969	29 180 788 552
1976	2 638	25 927 588 703
1977	2 969	29 180 788 552
1978	2 493	24 502 522 022

Table 8.9 : Yearly energy supply and demand by wildebeest plus their major competitors on the grasslands of Etosha (1973-78)

Year	Rainfall (mm)	Energy	Amount of energy (terajoules)	Theoretical balance as percentage of actual balance
1973	250	Actual supply	882	+144 %
		Theoretical demand	304	
		Balance: theoretical	+578	
		: actual	+401	
1974	701	Actual supply	2 137	+128 %
		Theoretical demand	335	
		Balance: theoretical	+1 802	
		: actual	+1 405	
1975	424	Actual supply	No data	-
		Theoretical demand	296	
		Balance: theoretical		
		: actual		
1976	577	Actual supply	2 365	+169 %
		Theoretical demand	257	
		Balance: theoretical	+2 108	
		: actual	+1 250	
1977	316	Actual supply	803	+128 %
		Theoretical demand	285	
		Balance: theoretical	+518	
		: actual	+404	
1978	590	Actual supply	1 494	+164 %
		Theoretical demand	268	
		Balance: theoretical	+1 226	
		: actual	+747	
Mean				147 %
SD				± 19 %
Mean underestimation of demand				58 %
Mean theoretical balance				+1 246 TJ
Mean measured balance				+841 TJ
Mean measured usage				695 TJ

which carry a heavy parasite load (Biggs, 1979, pers.comm.). An additional factor which contributed to the underestimated theoretical energy demand was the basis I used for calculating RMR and its various increments (Section 5). RMR was based on net energy requirements whereas the calculation of nutrient energy was based on metabolisable energy. Therefore this resulted in an overestimation of energy available in the food. According to Drodz (1975) not all the metabolisable energy is utilised for maintenance, activity, growth and reproduction. He estimated that 3 - 20 % of the gross energy is lost to the heat of the calorigenic effect of food, depending upon the type of forage ingested. Maynard and Loosli (1962) present data which show that feeds similar to those found in Etosha have a heat increment potential of 17 % of the metabolisable energy available to a ruminant. Also, Rogerson (1966, 1968) established that wildebeest used corrected metabolisable energy with an efficiency of 82 %, indicating that 18 % was lost to heat increment. Consequently, if my data are adjusted upward by 18 % to compensate for this difference between metabolisable energy and net energy the underestimation of demand (Table 8.9) is considerably reduced.

Finally, the basic formula which I used to calculate RMR, namely $70W_{kg}^{0,75}$ (NRC, 1966) is based on domestic ruminants and may be higher in wild ruminants such as wildebeest. For example, Rogerson (1966, 1968) has presented data showing that wildebeest may have an RMR of $104,3W_{kg}^{0,73}$ which suggested that they would require 20 - 30 % more metabolisable energy than domestic cattle. If this estimated increase in energy requirement is applied to my data in Table 8.9, then the underestimation is reduced further.

Thus, if all these factors which I consider likely to have caused the underestimation in energy demand are taken into account, the difference between my theoretical estimates and actual energy usage, as measured in exclusion and control plots, is gratifyingly small. It is therefore possible to accept the energy budgets with the above qualifications. Taking all these factors into consideration against a mean surplus of energy which is 1,2 times the requirement (Table 8.9), it is clear that errors in estimation of the demand could increase by a factor of 5,2 without exceeding the supply of energy. For example, in a low rainfall year (1973) the measured supply exceeded the measured usage by 183 % and in a year of high rainfall (1974) the supply exceeded the usage by 292 %. If bias for undercounting has not been totally removed and a large percentage of the residual grass is too short to be available to the herbivores, this surplus may be significantly reduced. Moreover, most of my estimates have been on the conservative side except for an important assumption that all the competitors eat only grass. This is not the case however and certain of the competitors, particularly springbok, utilise significant amounts of browse. In summary then, it would appear as if an adequate supply of energy exists for herbivores at Etosha. This is borne out by the good nutritional status of the majority of these animals (Section 9).

8.4.2 Protein Supply and Demand

The protein demand by the wildebeest population was based on data collected between 1976 - 78 (Section 6). Estimates for the period 1973 - 78 have been calculated in the same way and are given in Table 8.10. Protein supply and demand insofar as it affects the wildebeest and their major food competitors have been estimated for preferred grazing areas and are presented in Table 8.11.

The strong influence of season on the availability of crude protein is evident from the data. Seasonal influence on the levels of this critical nutrient in the forage is further influenced by years of rainfall extremes. For example, in 1977 rainfall was 75 % of average and in addition it was erratically distributed in time. Under

Table 8.10 : Estimated seasonal protein budgets for the wildebeest population on the grasslands of Etosha (1973 - 78)

Year	Population protein requirements (kg DM)			
	Seasonal totals			Yearly totals
	Wet, hot season (Jan. to April)	Dry, cold season (May to Aug.)	Dry, hot season (Sept. to Dec.)	
1973	61 431	58 114	54 433	173 978
1974	54 534	51 602	48 331	154 467
1975	49 070	46 429	43 257	138 756
1976	43 590	41 257	38 637	123 484
1977	49 070	46 429	43 257	138 756
1978	41 381	38 989	36 318	116 688

Table 8.11 : Seasonal protein supply and demand by wildebeest and their major competitors on the grasslands of Etosha (1973 - 78)

Year	Rainfall (mm)	Protein	Preferred grazing area			
			Wet season grazing (January to April)		Dry season grazing (May to December)	
			Protein in metric tons DM	Theoretical balance as % of measured balance	Protein in metric tons DM	Theoretical balance as % of measured balance
1973	250	Measured supply	3 283	+109 %	1 171	+ 28 %
		Theoretical demand	793		996	
		Balance: theoretical	+ 2 490		+ 175	
		: measured	+ 2 288		+ 617	
1974	701	Measured supply	11 641	+116 %	1 738	+ 77 %
		Theoretical demand	1 240		746	
		Balance: theoretical	+10 401		+ 992	
		: measured	+ 8 998		+ 1 287	
1975	424	Measured supply	No data	-	1 900	+ 87 %
		Theoretical demand	615		1 116	
		Balance: theoretical	-		+ 784	
		: measured	-		+ 900	
1976	577	Measured supply	12 504	+133 %	2 143	+150 %
		Theoretical demand	1 056		411	
		Balance: theoretical	+11 448		+ 1 732	
		: measured	+ 8 633		+ 1 154	

Table 8.11 (continued)

Year	Rainfall (mm)	Protein	Preferred grazing area			
			Wet season grazing (January to April)		Dry season grazing (May to December)	
			Protein in metric tons DM	Theoretical balance as % of measured balance	Protein in metric tons DM	Theoretical balance as % of measured balance
1977	316	Measured supply	2 215	+105 %	1 284	+ 42 %
		Theoretical demand	427		939	
		Balance: theoretical	+ 1 788		+ 345	
		: measured	+ 1 707		+ 818	
1978	590	Measured supply	7 519	+132 %	1 469	+144 %
		Theoretical demand	1 086		385	
		Balance: theoretical	+ 6 433		+ 1 084	
		: measured	+ 4 862		+ 751	
Mean			119 %		88 %	
SD			± 13 %		± 51 %	
Mean estimation of demand			Underestimate of 43 %		Overestimate of 10 %	
Mean theoretical balance			6 512 TJ		953 TJ	
Mean measured balance			5 298 TJ		921 TJ	
Mean measured usage			2 135 TJ		697 TJ	

these conditions, measured supply of crude protein was 18 % of the previous year when rainfall was 577 mm, which is 138 % above average.

As in the case of the energy supply and demand, there appeared to be no shortage of protein during the wet, hot season. My mean, theoretical estimate of demand for five years was 43 % below the usage as measured by exclusion plots. Factors contributing towards this underestimate were *inter alia* the protein cost of supporting a heavy parasite load in the case of zebra (Biggs, 1979, pers. comm.) and the fact that I used the basic formula of $70W_{kg}^{0,75}$ (NRC, 1966) in the calculation of endogenous urinary nitrogen (Section 8.2.4). As discussed under the energy balance, wildebeest and their competitors may have a higher RMR than the standard formula used for this investigation (Rogerson, 1966, 1968). In addition, the protein requirements for gestation were based on domestic cattle and sheep, which could have contributed to the underestimation of protein demand in Etosha's free-ranging ungulates and zebras. Nevertheless, the mean measured balance of protein was 2,5 times greater than the mean usage as measured by exclusion plots (Table 8.11) and errors in my estimation of demand could still increase by a factor of 8,0 on average, without exceeding the protein supply. In the two years where rainfall was below average

(1973, 1977) my estimates of protein demand were closest to the measured demand (20 % and 16 % underestimate respectively). This was probably because the poor production of grass caused some herbivores, notably springbok, to switch to alternative sources of protein, namely browse. This premise is supported by my field observations and is also reflected in the energy demand calculated for 1977 (Table 8.9). Even so, under these conditions of lowered grass production, the measured balance exceeded the measured usage by factors of 2,9 (1973) and 4,0 (1977) respectively.

The situation during the protracted dry period, lasting up to eight months at Etosha, is notably different to the abundant quantities of protein available during the wet season of four months. It is evident that my mean estimate of demand exceeded the mean measured usage by a factor of 1,1 for four of the six years (Table 8.11). Since the estimates of the yearly energy demand as well as the protein demand for the wet season were well below the usage as measured by exclusion plots, my estimates during the dry seasons indicate that some of the herbivores had changed from grazing to browsing. This surmised change in diet was confirmed by an observed movement of zebra and springbok from the grasslands to adjoining mopane savanna in the dry season. During two years (1976, 1978) very good rains resulted in high grass productivity, keeping herbivores on the open plains for most of the seasonal year. Consequently, my estimates of demand are about 50 % below the measured usage which is of similar magnitude to the underestimate for the wet seasons when protein was freely available.

A point I wish to stress is that while the major competitors were able to include browse in their diet when protein levels dropped during the dry, hot season, wildebeest were confined to the open grasslands because of their preference for short grass. Thus the catholically foraging zebra and springbok which comprised the greatest live mass of herbivores, would be able to withstand serious depletions of grass protein more successfully than the specialised wildebeest. A definite possibility of protein deficiency exists for wildebeest during the nadir of grass production, particularly in years of poor rainfall. However, the surplus protein which is usually available during the wet season probably enables wildebeest to build up body reserves which can be tapped during times of nutritional stress. Also, the ruminating wildebeest can rely on its ability to recycle urea. Therefore, although I do not consider the protein factor to be a gross problem at Etosha, and certainly not one which could have limited the wildebeest population during the six years under review, protein has been identified as a possible critical factor for grazers at Etosha. It is also significant that the maximum demand for protein by wildebeest, namely during peak lactation, does not occur during the critical period of supply.

A sensitive dry season grazing area which could be the pivotal factor in wildebeest nutrition during a drought is the Etosha Pan itself. This became clearly evident as my investigation, which took place in a wet cycle, progressed. The Pan produced up to 20 000 hectares of protein-rich, short grass, namely *Sporobolus tenellus*, which appeared to be preferred by wildebeest above all other grazing. They chose to forage this species even at a residual biomass of only 4,0 g/m^2 in preference to the coarser *Sporobolus spicatus* which grew in profusion on the adjacent plains. For example, during an aerial census in September 1978, a total of 1 629 out of 2 493 wildebeest (65 % of the population) had moved onto the Etosha Pan where *Sporobolus tenellus* occurred in pure stands. It is, however, possible that the likelihood of decreased predation was also a reason for wildebeest preferring the Pan. The failure of this area, which in 1978 accounted for 44 % DM of the total grass produced by the dry season grazing areas, could nevertheless result in a critical protein shortage for wildebeest. This would be aggravated by the present fenced boundaries of Etosha which prevent wildebeest from migrating to their traditional dry season grazing areas in Owambo to the north. In this context it should be remembered that Etosha's boundaries were completely fenced in 1973 and that since then the wildebeest population has not been exposed to severe drought.

In addition to critical absolute amounts of protein, the level of protein in the grass falls below critical levels at certain seasons of the year. This has been discussed in detail in Section 7.4.3.

8.4.3 Nutrient Supply in Relation to Drinking Water

In addition to the aforegoing considerations, I wish to underline the fact that wildebeest, being obligate drinkers, were limited to a maximum recorded radius of 15 km from water during the dry season (Section 7.4.8). Thereby the daily drinking habit of wildebeest imposes restrictions on their foraging ability, and although grass may exist in the dry season, it may not be available to wildebeest. Clear evidence of water as a factor limiting wildebeest grazing patterns was found on the Etosha Pan during dry seasons. In this situation the available drinking water came from natural, contact fountains which flow perennially at the edge of the Pan. At the height of the dry season (September) a survey of wildebeest on the Pan (n = 453) showed that 28 % were between 10 and 15 km from the nearest available waterhole; the remaining 72 % were less than 10 km from water. This agrees closely with Western's (1975) findings in the arid Amboseli ecosystem of Kenya where all the wildebeest were found within 12 km of water and 99,5 % of the biomass density of water dependent species were nearer than 15 km to water. However, on the Etosha Pan I found that springbok, gemsbok and ostrich occur up to 24 km from drinking water and this would favour their survival during a drought when compared to wildebeest. Zebra were not often recorded on the Pan and then occurred less than 10 km from water. In the mopane savanna which is preferred habitat for zebra during the dry season, I recorded them, and also red hartebeest, up to 20 km away from water (cf. 16 km for zebra recorded by Western, 1975). They too, therefore appeared to forage further from water than wildebeest.

Consequently, because of this varying water-food dependence, competitors of wildebeest at Etosha may have greater capacity for survival when nutrient availability becomes critical. Evidence of wildebeest's sensitivity to drought has been presented on several occasions (Van der

Spuy, 1960; Child, 1972b; Hillman and Hillman, 1977). Management plans at Etosha should take into account the susceptibility of wildebeest to drought conditions when the food-water link may become critical.

8.5 SUMMARY

8.5.1

The energy and protein requirements of the major food competitors of wildebeest at Etosha were estimated by applying formulae used for establishing these demands in free-ranging wildebeest. This made it possible to give an approximation of the total demand of energy and protein by the large herbivores. By balancing the measured supply of these critical nutrients against the estimated demand as well as against the measured usage, it was clearly evident that sufficient energy was available, but that protein, particularly protein percentage, could become a critical factor during a dry climatic cycle.

8.5.2

Aerial censuses were used to estimate the total populations of the five major competitors, namely

Burchell's zebra, springbok, gemsbok, red hartebeest and ostrich. Correction factors were applied to these counts to compensate for undercounting bias. Age-sex ratios of the competitors were established and applied to the corrected population estimates in order to provide a more refined measure of live mass for calculating energy and protein requirements.

8.5.3

In the case of mammalian competitors, total energy demand was estimated by applying an increment of 2,0 over RMR which was based on the findings in wildebeest. Total protein demand was calculated for maintenance, growth, gestation and lactation, using suitably modified equations developed for domestic animals. In the case of ostrich, total energy demand was calculated by first taking 1,9 times RMR for non-passerine birds and then adding the total energetic cost of egg production and incubation to hens, as well as the cost of incubation to cocks. Protein demand in ostrich was estimated by using modified equations to allow for maintenance, growth and egg production.

8.5.4

A feature of the theoretical estimate of energy demand for the grazing herbivores, including wildebeest, was that it consistently underestimated the measured usage by an average of 58 %. However, when compensatory factors such as reduction of metabolisable energy in the grass to net energy, the cost of rumination, parasitism and certain aspects of homeothermy were taken into account, the margin of underestimation was substantially reduced. In addition, the basic formula of $70W_{kg}^{0,75}$ used to calculate RMR in the free-ranging competitors and in wildebeest may have contributed to the underestimation of energy demand. Nevertheless, the measured energy balance was 1,2 times greater than the measured usage and errors in estimation of demand could have increased by a factor of 5,2 before exceeding the measured supply of energy. Consequently, energy was not considered to be a limiting factor for wildebeest or for their food competitors during the period 1973 - 78.

8.5.5

The strong seasonal influence of rainfall on protein levels in the grasslands of Etosha resulted in an abundance of this nutrient for wildebeest and their competitors during the four-month wet season. Again, the theoretical demand underestimated the measured usage by 43 % and may have been due to the omitted cost of parasitism especially in zebra, and the under-calculation of endogenous urinary nitrogen and the nitrogen required for gestation and lactation. During the wet season, a surplus of protein was reflected by the measured balance which exceeded the measured usage by 2,5 times.

The lengthy dry season of eight months was identified as a period when protein deficiency could occur. Although no negative balance was found for the period 1973 - 78, which was characterised by good rainfall, negative protein balance could occur during a drought situation. Wildebeest were considered to be more susceptible to protein deficiency in grass than other herbivores because of their inability to incorporate significant amounts of browse in their diet. The Etosha Pan itself was the most important dry season grazing area for wildebeest during the study, but it could fail entirely to produce a stand of *Sporobolus tenellus* in times of drought. This halophytic perennial is the only grass capable of growing in the present, highly saline conditions existing in the Etosha Pan. In the event of severe drought, the closure of traditional migration routes by fences and the failure of the dry season grazing areas in Etosha could result in a critical deficiency of protein for grazers such as wildebeest.

8.5.6

The susceptibility of wildebeest to drought was further underlined by their daily water requirement which imposed on them a maximum recorded foraging limit of 15 km from water. Their major food competitors were all capable of foraging beyond this limit and this would have survival value if the water-food link were to become critical during drought conditions.

8.5.7

The overall finding of this investigation was that the Etosha wildebeest population was not nutritionally stressed during the period 1973 - 1978, before which no suitable data exist to make conclusions. In making this inference, it was necessary to take into account the fact that the period of investigation was dominated by years of above average rainfall and that the supply of nutrients was consequently liberal. The danger of critical nutrient deficiency in wildebeest is likely to exist during a prolonged drought.

Section 9

NUTRITIONAL STATUS

9.1 INTRODUCTION

This investigation was designed to assess the nutritional status of Etosha's wildebeest population, on a seasonal basis. Nutritional status or "condition" indicates the ability of an animal to withstand internal stresses, such as disease or sexual activity, and external stress factors, such as reduced food or water quality, predation and changes in climate (Sinclair, 1977). Wildebeest whose nutritional status is at a high level will be better able to withstand internal and external stresses to which they are exposed. Inability to do this may result in the death of the animal as has been shown by massive die-offs of wildebeest populations during droughts (Van der Spuy, 1960; Child, 1972b; Hillman and Hillman, 1977). Consequently, I attempted an objective assessment of the condition of individuals from the Etosha population, using internal examinations to predict their chances of survival. Because detailed internal examination is time consuming, I also subjectively assessed the external physical condition of a large and representative sample of the population at critical seasons.

9.2 METHODS

9.2.1 Visual Ratings

Since the external physical appearance of an ungulate is a good indicator of its nutritional status (Riney, 1960), I used five mutually exclusive categories whereby the nutritive level of wildebeest could be subjectively measured. These categories were based on a technique which was successfully employed on a population of free-living gemsbok (Hamilton *et al.*, 1977). The physical appearance of a wildebeest was judged by the degree to which the skeletal details of its body were visible (Fig. 9.1) and points were awarded on this basis. Thus :

5 (excellent) = hindquarters well rounded and no ribs showing; general appearance in relation to posture and coat sheen excellent

4 (good) = hindquarters rounded, but ribs show slightly

3 (fair) = hindquarters angular in appearance and ribs well defined

2 (poor) = pelvic bones prominent and ribs protrude

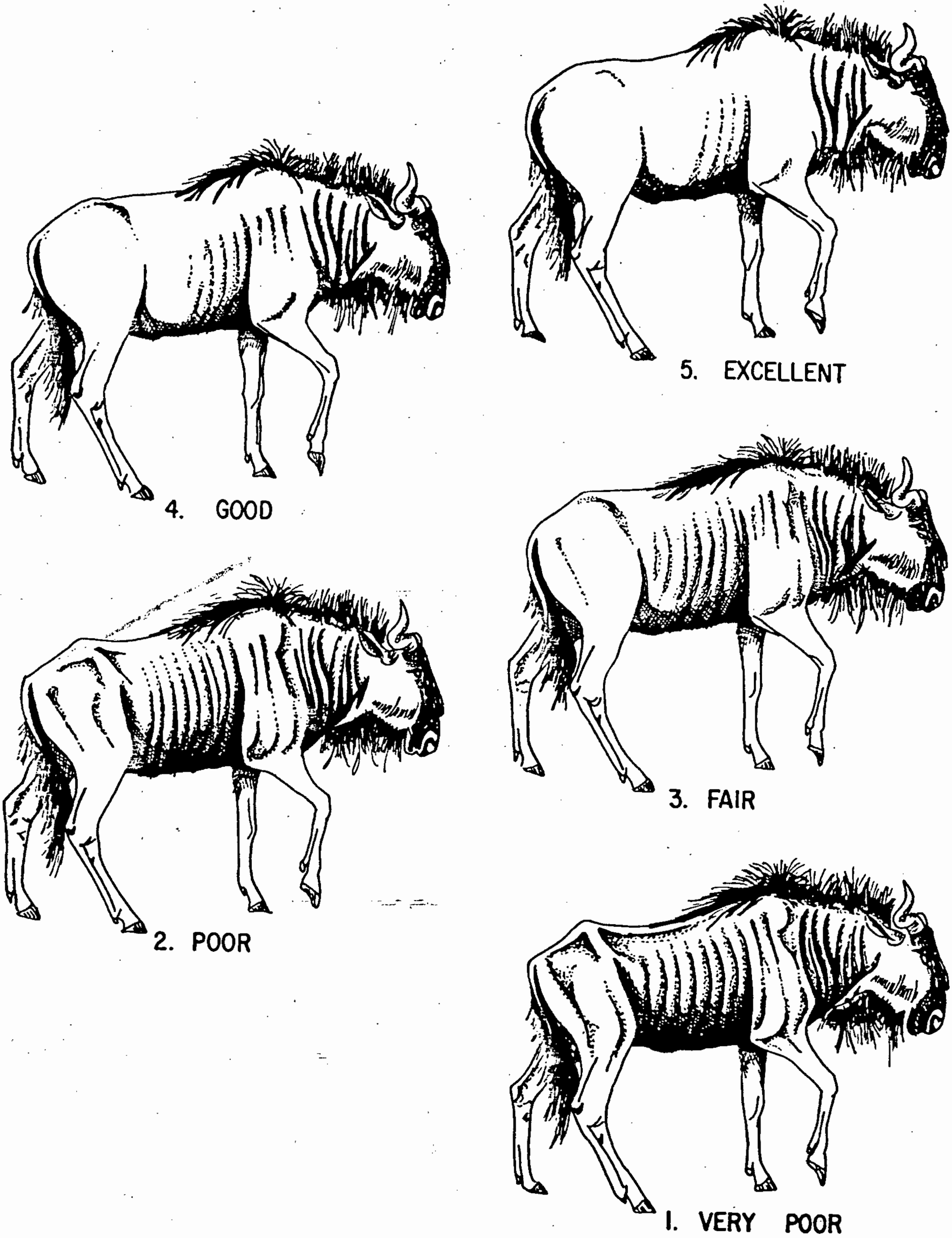

Fig. 9.1 : Diagrammatic presentation of the five categories used to estimate the nutritional status of wildebeest at Etosha (1976-79).

1 (very poor) = skeletal details clearly visible and rump concave; general appearance, posture and coat condition deteriorated.

It is evident from these categories, that wildebeest in class "1" or "2" condition would be less likely to survive than those occupying classes "3", "4" and "5". Although the allocation of a condition category on this basis is subjective, these five classes were easily distinguishable in the field and, with practice, a wildebeest could be rapidly classified. In total I carried out visual ratings on 67 marked wildebeest, which were resighted at regular intervals, and on the population (n = 3 898) during the period 1977 - 78.

9.2.2 Kidney Fat

The amount of perinephric fat, expressed as a percentage of the kidney mass has been widely used to assess the nutritive level of ungulate species including buffalo (Sinclair, 1977) and wildebeest (Attwell, 1977). Kidneys from 19 shot wildebeest (Section 10), with the surrounding fat suitably trimmed (Attwell, 1977) were measured to the nearest 0,01 g. The kidney fat index (KFI) was then determined using the methods of Riney (1955) and N.S. Smith (1970) and expressed as :

$$\text{KFI} = \frac{\text{perinephric fat mass}}{\text{kidney mass}} \times 100.$$

9.2.3 Bone Marrow Fat

Bone marrow fat is the last reserve of stored energy to be utilised when an animal is exposed to nutritive stress (Sinclair and Duncan, 1972). Consequently, it is a critical measurement of condition when stress becomes extreme. Moreover, when bone marrow dry mass of wildebeest was expressed as a percentage of its wet mass, a linear relationship with the fat content of the bone marrow was found to exist (Sinclair and Duncan, 1972). In addition, they found that bone marrow could be visually rated to give a rapid classification of the nutritive level of an ungulate if more refined techniques could not be applied.

During the present study, I collected between five and 20 g of fresh bone marrow from 20 wildebeest which had been shot, or killed by lions. Marrow from the tibia or femur was measured to the nearest 0,01 g before being oven-dried at 100 °C to a constant mass. Loss in moisture was then calculated and the fat in the dried marrow was extracted with hot ether for six hours by Soxhlet reflux. The ether was subsequently evaporated and the dry fat residue was measured to the nearest 0,01 g. Fat content was then compared to the percentage dry mass/wet mass of the original marrow sample to establish whether they were related.

9.2.4 Blood Analyses

The possibility of using blood constituents as indicators of nutritional status in ungulates has not given consistent results (N.S. Smith, 1970) and in the case of wildebeest, no relationship could be found between packed cell volume (PCV) and KFI or percentage bone marrow fat (Attwell, 1977). However, studies on Alaskan moose indicated a relationship between several blood parameters and the nutritive level of the animal (Franzmann and LeResche, 1978). To investigate whether a similar relationship existed in the case of Etosha wildebeest, blood was taken from 59 immobilised and seven shot animals, on a seasonal basis, over a two-year period (1977 - 78). Blood samples were collected from the jugular or heart in a heparinised, disposable syringe. The plasma was drawn off after 15 minutes of centrifuging in a portable, clinical centrifuge set at 7 000 rpm and immediately cooled to -20 °C (± 2 °C) using carbon dioxide. The samples were subsequently transferred to a laboratory where they were stored at the same temperature. Analyses were done by auto-analytic methods (Model SMA 12/60) and the results recorded on charts (No. 940-0859-02A).

9.2.5 Liver Analyses

Sections of liver from 21 shot wildebeest were preserved in 10 % formol-saline. They were analysed for macro-elements and trace elements by the Veterinary Research Institute, Onderstepoort and the Veterinary Regional Laboratory, Windhoek. Eight of the samples were also submitted to the Atomic Energy Board (Republic of South Africa) for analysis of zinc, cobalt and selenium. All liver analyses were converted to dry mass and the values expressed in umol/l.

9.2.6 Haemocytology

Blood smears, taken peripherally from 23 shot wildebeest, were prepared and stained with Giemsa, according to Coles (1967). The smears were examined under an illuminated 100-magnification microscope for anaemia and other haemocytic abnormalities.

9.3 RESULTS AND DISCUSSION

9.3.1 Visual Physical Condition

To simplify the presentation of data, I distinguished between adult bulls, adult cows, immatures (1 - 2 years old) and calves (< 1 year), and expressed the visual ratings of nutritional status as a percentage for nine seasons (1976 - 1979). The results are shown in Tables 9.1 to 9.4.

A negligible number of wildebeest (< 2 % of the total observations) were in a poor or very poor condition. Moreover, those in very poor condition had injured legs and were limping badly, or were calves which had been separated from their mothers. Animals in a fair condition comprised 21 % of all observations, whilst the majority (62 %) were in good condition. The category of excellent condition was awarded to 16 % of all animals observed.

I applied the t statistic for two means to test for significant differences in nutritional status within and between age-sex classes. In all cases, more wildebeest were in good condition than in fair condition ($P < 0{,}02$). Similarly, there were more animals in good condition than

Table 9.1 : Visual physical condition of adult wildebeest bulls at Etosha on a seasonal basis (1976 - 79)

Year	Season	*Visual rating (%)					Rainfall as % of average
		Very poor	Poor	Fair	Good	Excellent	
1976	Dry, cold	0	0	50	28	22	161
	Dry, hot	0	0	29	43	28	
1977	Wet, hot	0	0	17	67	16	
	Dry, cold	0	0	34	53	13	60
	Dry, hot	0	4	46	48	2	
1978	Wet, hot	0	0	18	60	22	
	Dry, cold	0	0	19	56	25	112
	Dry, hot	0	0	32	52	16	
1979	Wet, hot	0	0	17	61	22	110
Mean		0	<1	29	52	18	111

* n = 1 103 observations

Table 9.2 : Visual physical condition of adult wildebeest cows at Etosha on a seasonal basis (1976 - 79)

Year	Season	*Visual rating (%)					Rainfall as % of average
		Very poor	Poor	Fair	Good	Excellent	
1976	Dry, cold	0	0	21	52	27	161
	Dry, hot	0	0	19	62	19	
1977	Wet, hot	0	0	40	54	6	
	Dry, cold	0	0	18	37	45	60
	Dry, hot	0	2	21	51	26	
1978	Wet, hot	0	1	41	53	5	
	Dry, cold	2	1	13	48	36	112
	Dry, hot	0	8	8	73	11	
1979	Wet, hot	0	10	17	40	33	110
Mean		<1	2	22	52	23	111

* n = 1 234 observations

Table 9.3 : Visual physical condition of immature wildebeest aged one to two years at Etosha on a seasonal basis (1976 - 79)

Year	Season	*Visual rating (%)					Rainfall as % of average
		Very poor	Poor	Fair	Good	Excellent	
1976	Dry, cold	0	0	16	65	19	161
	Dry, hot	0	0	21	75	4	
1977	Wet, hot	0	0	18	69	13	60
	Dry, cold	0	0	17	60	23	
	Dry, hot	0	0	21	74	5	
1978	Wet, hot	0	0	7	92	1	112
	Dry, cold	0	0	15	74	11	
	Dry, hot	0	0	26	70	4	
1979	Wet, hot	0	0	19	77	4	110
Mean		0	0	18	73	9	111

* n = 540 observations

Table 9.4 : Visual physical condition of wildebeest calves, less than one year old, at Etosha, on a seasonal basis (1976 - 79)

Year	Season		[x]Visual rating (%)				Rainfall as % as average
		Very poor	Poor	Fair	Good	Excellent	
1976	Dry, cold	0	1	4	91	4	161
	Dry, hot	0	0	32	49	19	
1977	Wet, hot	1	1	9	85	4	
	Dry, cold	<1	<1	4	91	4	60
	Dry, hot	0	0	33	51	16	
1978	Wet, hot	<1	<1	9	87	3	
	Dry, cold	0	0	31	46	23	112
	Dry, hot	0	0	25	58	17	
1979	Wet, hot	0	<1	17	77	6	110
Mean		<1	<1	18	71	10	111

[x] n = 1 021 observations

in excellent condition ($P < 0,01$). The number of adults in excellent condition did not differ significantly from the number in fair condition ($P > 0,05$), but there were more immatures and calves in fair condition than in excellent condition ($P < 0,05$). This may have been due to growth stress. When adult bulls were compared to adult cows and immatures were compared to calves, there was no difference in the number of animals judged to be in fair or good or excellent condition ($P > 0,05$). Similarly, there was no difference in the number of adults in fair condition compared to the number of immatures and calves. However, significantly more young animals were in good condition than adults; conversely, more adults than young were in excellent condition ($P < 0,01$).

Tests for seasonal differences in the nutritive level of all age-sex classes showed that more wildebeest were in excellent condition during the dry, cold season than during the wet, hot season ($P < 0,05$). This may have been due to the stresses imposed by sexual activity in bulls and lactation in cows, which were maximal in the wet, hot season. Furthermore, wildebeest may only have shown the benefits of improved nutrition in the wet season during the subsequent dry, cold season. No other seasonal differences were found in the number of animals in good or fair condition.

Judged by their external physical appearance, it therefore appears that the wildebeest population was at no stage under serious nutritive stress during the study. The rainfall during this period was well above average, except during 1977 when it was 60 % of average. Nevertheless, the visual condition of the majority of wildebeest was good throughout 1977 and this may have been influenced by a succession of above average rainy seasons, commencing 1974, which resulted in correspondingly high productivity of grass.

9.3.2 Kidney Fat Index

The age-sex and social status of 16 shot wildebeest was related to their KFI. Their external condition was judged visually before shooting. The results are shown in Table 9.5. No significant difference existed between wet and dry season KFI values ($t = 0{,}39$ and $P > 0{,}05$). The external physical condition appeared to be related to the KFI in 15 out of 16 cases. The exception occurred during the wet season when a two-year old bull was judged to be in good condition, but had a low KFI value of 9,0 %. This may have been due to the demands made on the animal at a transitory stage of its social status, namely expulsion from a mixed herd. However, the KFI may not always be a valid indicator of nutritional status

Table 9.5 : Kidney fat index of wildebeest at Etosha, on a seasonal basis (1978)

Season	Age-sex and social status	Visual condition rating	Kidney fat index (%)*	
			Individual	Mean
Wet	One-month old cow	Excellent	38,7	25,1
	One-year old cow	Fair	9,0	
	One-year old bull	Fair	8,7	
	Two-year old cow	Good	26,2	
	Two-year old bull	Good	9,0	
	Adult cow, not lactating	Excellent	59,9	
	Adult cow, lactating	Fair	6,7	
	Adult, territorial bull	Excellent	42,3	
Dry	9-month old cow	Excellent	20,3	22,3
	9-month old bull	Good	19,9	
	21-month old cow	Excellent	42,0	
	21-month old bull	Good	27,1	
	Adult cow, pregnant	Poor	9,6	
	Adult cow, pregnant	Excellent	41,1	
	Adult cow, lactating	Poor	7,6	
	Adult, bachelor bull	Good	10,6	

* $\text{KFI} = \frac{\text{Perinephric fat mass}}{\text{kidney mass}} \times 100$

(N.S. Smith, 1970; Attwell, 1977) especially in growing animals. Also, errors in the calculation of the KFI can occur from inconsistent trimming of perinephric fat (Attwell, 1977).

In the dry season, two adult cows, both about six months pregnant had KFI values of 9,6 % and 41,1 %. This considerable difference may have been due to their age difference. Based on tooth-wear criteria of wildebeest (Watson, 1967), the cow with the lower KFI value was aged at 10 - 15 years (condition rating poor), while the cow with the higher KFI value was aged at 4 - 5 years (condition rating excellent). There is disagreement in the literature about the relationship of kidney fat and reproduction. For instance, Sinclair and Duncan (1972) found that fluctuations in wildebeest kidney fat reflected reproductive activity but no such relationship was apparent in wildebeest examined by Attwell (1977). Because of such widely differing results, coupled with the possible influence of age on the nutritive level of a pregnant wildebeest as indicated in my study, it seems advisable to treat KFI values with caution. This view is strengthened by the fact that kidney fat in growing wildebeest (< 3 years old) is also considered unsuitable as an indicator of seasonal nutritional status (Attwell, 1977; Table 9.5 of this investigation).

From the results of my study it is concluded that KFI values should preferably be interpreted in conjunction with visual ratings of condition and a more critical parameter, such as bone marrow fat, when establishing the nutritional status in wildebeest.

9.3.3 Relationship of Bone Marrow Fat to Nutritional Stress

Earlier investigations of wildebeest bone marrow fat in relation to dry mass of the marrow have produced very similar regression equations of $y = 1{,}0042x - 7{,}2829$ (Sinclair and Duncan, 1972) and $y = 1{,}0047x - 5{,}76$ (Attwell, 1977). They concluded that these predictions support the generalised equation proposed for most ungulates, namely :

% marrow fat = % dry mass -6 (Sinclair and Duncan, 1972)

The results of my study (Table 9.6) are inconsistent with these findings and gave a relationship of $y = 0{,}90x + 20{,}07$ ($r = 0{,}70$) which reflects a considerable amount of scatter of the data around the regression line. Consequently, my findings did not indicate a reliable relationship between marrow fat and dry mass of marrow. This aspect requires further investigation at Etosha, but this was not possible

Table 9.6 : Bone marrow fat in wildebeest at Etosha on a seasonal basis (1978)

Season	Age-sex and social class	Visual ratings		Bone marrow analyses	
		Physical condition	Marrow colour^{x}	Percentage fat	$\frac{\text{Dry mass}}{\text{Fresh mass}} \times 100$
Wet	One-month old cow	Excellent	White, opaque	92,52	78,57
	Two-month old bull	Very poor	Pink, gelatinous	^{xx} 3,01	13,49
	One-year old cow	Fair	White, opaque.	94,53	58,61
	One-year old bull	Fair	White, opaque	95,69	66,22
	Two-year old cow	Good	White, opaque	94,52	74,50
	Two-year old bull	Good	White, opaque	88,04	40,58
	Adult cow, not lactating	Excellent	White, fatty	96,95	89,78
	Adult cow, lactating	Fair	Pink, opaque	69,33	24,65
	Adult bachelor bull	Excellent	White, fatty	95,83	87,18
	Adult territorial bull	Excellent	White, fatty	99,08	93,65
Mean		-	-	91,83	68,19
SD		-	-	± 8,98	± 23,39

Table 9.6 (continued)

Season	Age-sex and social class	Visual ratings		Bone marrow analyses	
		Physical condition	Marrow colour[x]	Percentage fat	$\frac{\text{Dry mass}}{\text{Fresh mass}} \times 100$
Dry	Three-month old cow	Very poor	Pink, gelatinous	[xx] 2,29	8,71
	Eight-month old cow	Excellent	White, opaque	96,66	80,63
	21-month old cow	Excellent	White, opaque	60,11	85,88
	21-month old bull	Good	White, opaque	98,48	84,95
	Adult cow, pregnant	Poor	Pink, opaque	78,83	61,09
	Adult cow, pregnant	Good	White, fatty	91,45	79,62
	Adult cow, pregnant	Excellent	White, fatty	98,29	94,23
	Adult bull, bachelor	Good	White, fatty	85,48	72,20
	Adult bull, territorial	Fair	Pink, opaque	39,37	21,55
	Adult bull, territorial	Fair	Pink, opaque	39,45	25,41
Mean		-	-	76,46	62,07
SD		-	-	± 24,22	± 28,47

[x] According to Sinclair and Duncan (1972)

[xx] Values not included in calculation of the means; explanation given in text

during the present study due to the limited number of fresh bone marrow samples. However, for the purpose of this thesis, it was sufficient to test the data for seasonal and age-sex differences in bone marrow fat. Applying the t statistic for two means, I found no significant difference in fat content of the marrow during the wet and dry seasons ($P > 0,05$). Similarly, there was no difference between the sexes or between immatures and adults. The level of marrow fat was above 80 % in 13 of the 20 samples, indicating that the environmental stresses at Etosha were not sufficiently severe to cause mobilisation of marrow fat reserves.

The seven marrow samples which had a marrow content of less than 80 % (Table 9.6) deserve closer scrutiny. Two samples (69,33 % and 78,33 % fat) were from adult cows which were respectively lactating and pregnant, and so the lower values may have been linked to the considerable physiological stress they were experiencing. The KFI of these cows was 6,7 % and 9,6 % respectively (Table 9.5) which is consistent with the findings of Sinclair and Duncan (1972), namely that kidney fat is mobilised before bone marrow fat. A 21-month old cow with a marrow fat content of 60,11 % was in direct contrast to a bull of the same age which had a value of 98,48 %. No explanation for this is immediately apparent, since the KFI of these two animals appears to contradict the marrow fat levels. For instance, the cow's KFI was 42,0 %, whilst the bull's was 27,1 %. This example emphasises the necessity to approach the kidney fat and marrow fat indices with circumspection because of individual variation which may occur. In this regard Hanks *et al.* (1976) have drawn attention to the fact that such indices may be oversimplified evaluations of complicated physiological processes which are incompletely understood. In the case of two adult territorial bulls the marrow fat contents were very similar at 39,37 % and 39,45 %. Both animals were killed by lions at the end of the rutting season (May) and the stress attending a peak of sexual activity is clearly evident. Unfortunately no KFI could be calculated from these bulls because of predation. The two lowest marrow fat values obtained (2,29 % and 3,01 %) were from calves which had been purposely sampled after they had lost their mothers. They were consequently not included in the calculation of seasonal means of marrow fat (Table 9.6). Nevertheless, their very low values and the visual ratings of their condition confirmed that extreme stress, in this case starvation, was reflected by the extent to which their last fat reserves were mobilised. It is unlikely that they would have survived.

In conclusion, the findings of this investigation showed that most of the wildebeest sampled had adequate marrow fat reserves throughout the year. This indicated that they were not subjected to extreme nutritional stress and that where depletion of these critical reserves of energy had occurred, it could usually be related to reproduction.

9.3.4 Blood Status

Blood analyses of Etosha's wildebeest are given in Table 9.7 and Appendix 38.

9.3.4.1 Plasma Proteins

The plasma samples from wildebeest (n = 66) had a total protein mean value of 69,65 g/l ± 7,49 (range 44,5 - 85,0). Bulls (n = 42) contained 70,77 g/l total plasma protein (TPP) which was very similar to the normal bovine male level for 18 - 30 month-old animals of 69,7 g/l (Coles, 1967). Similarly, cows (n = 24) contained 67,69 g/l compared to the normal bovine female level for five to nine-year old animals of 75,6 g/l (Coles, 1967). This lower level in Etosha's wildebeest cows may have been induced by growth in young animals or by pregnancy, which may lower the circulating levels of proteins, particularly albumin (Doxey, 1971). However, the albumin level of

Table 9.7 : Nutritional status of wildebeest at Etosha as reflected by analyses of blood plasma (1976 - 78)

Measurement	Blood plasma constituent						
	Total protein (g/l)	Albumin (g/l)	Total calcium (mmol/l)	Bound calcium (mmol/l)	Ionised calcium (mmol/l)	Inorganic phosphorus (mmol/l)	Cholesterol (mmol/l)
All seasons :							
Maximum	85,00	46,50	3,02	1,68	1,34	2,82	3,04
Minimum	44,50	29,00	1,16	0,65	0,51	0,72	1,10
Mean	69,65	36,42	2,41	1,34	1,07	1,47	1,80
± SD	7,49	4,28	0,31	0,17	0,14	0,51	0,35
Wet season mean	67,05	34,30	2,37	1,32	1,05	1,73	1,85
Dry season mean	71,04	37,55	2,44	1,37	1,08	1,33	1,78
t^x	- 2,12	- 3,13	-0,85	-1,04	-0,83	3,19	0,69
P^{xx}	< 0,05	< 0,01	>0,10	>0,10	>0,10	<0,01	>0,10
Bulls: mean	70,77	36,81	2,43	1,35	1,08	1,37	1,78
Cows : mean	67,69	35,73	2,38	1,33	1,06	1,64	1,84
t^x	1,63	0,99	0,62	0,41	0,60	-2,13	-0,70
P^{xx}	> 0,10	> 0,10	>0,50	>0,50	>0,50	<0,05	>0,10
Adults: mean	71,12	37,20	2,43	1,35	1,08	1,35	1,82
Immatures: mean	64,44	34,49	2,37	1,32	1,05	1,75	1,75
t^x	3,01	2,41	0,74	0,73	0,80	-3,03	0,76
P^{xx}	< 0,01	< 0,02	>0,10	>0,10	>0,10	<0,01	>0,10

Table 9.7 (continued)

Measurement	Blood plasma constituent					
	Urea (mmol/l)	Urates (mmol/l)	Total bilirubin (umol/l)	Conjugated bilirubin (umol/l)	Alkaline phosphatase (Mu/ml)	Glutamic oxalacetic transaminase (mU/ml)
All seasons :						
Maximum	12,25	0,15	4,50	1,00	370,00	300,00
Minimum	3,25	0,01	1,90	0,00	18,00	109,00
Mean	6,57	0,05	2,78	0,03	99,24	161,26
± SD	1,68	0,03	0,56	-	80,84	37,05
Wet season mean	8,06	0,07	2,74	0,09	134,70	178,65
Dry season mean	5,78	0,05	2,79	0,00	80,28	151,95
t^{*}	5,85	2,94	-0,37	-	2,73	2,95
p^{**}	<0,01	<0,01	>0,50	-	< 0,01	< 0,01
Bulls: mean	6,25	0,05	2,76	0,02	94,48	165,45
Cows: mean	7,14	0,05	2,82	0,04	107,58	153,92
t^{*}	-1,92	0,28	-0,43	-	- 0,63	1,22
p^{**}	>0,05	>0,50	>0,50	-	> 0,50	> 0,10
Adults: mean	6,58	0,05	2,78	0,00	72,09	160,79
Immatures: mean	6,56	0,05	2,78	0,11	166,42	162,42
t^{*}	0,04	0,50	0,02	-	- 5,03	- 0,16
p^{**}	>0,50	>0,50	>0,50	-	< 0,01	> 0,50

* t = t statistic for two means; ** p = probability level

bulls ($\overline{x}$ = 36,81 g/l) and cows ($\overline{x}$ = 35,73 g/l) at Etosha did not differ significantly (t = 0,99; P > 0,05). Neither was there a difference in the TPP of bulls and cows. But adults (n = 47) had a significantly higher level of TPP ($\overline{x}$ = 71,12 g/l) than immatures (n = 19) ($\overline{x}$ = 64,44 g/l) at P < 0,01. Also, the albumin in adult plasma ($\overline{x}$ = 37,20 g/l) was at a higher level than that of immatures ($\overline{x}$ = 34,49 g/l) at P < 0,01. This indicated that growth stress rather than pregnancy may have impinged upon the circulating levels of TPP and its major fraction, namely albumin.

When the combined sexes were examined on a seasonal basis, there were significantly higher (P < 0,01) levels of TPP circulating during the dry season ($\overline{x}$ = 71,04 g/l) than the wet season ($\overline{x}$ = 67,05). This was contrary to the levels of crude protein existing in the forage at these seasons (Section 7.4.4) but was in accordance with my findings (Section 7.4.5) that faecal crude protein was significantly higher during the dry season than the wet season. I ascribed this to factors such as food selection and the ability of ruminants to synthesize their protein from non-protein nitrogenous compounds via microbial action in the rumen.

The albumin fraction of Etosha's wildebeest plasma protein ($\overline{x}$ = 36,42 g/l) was higher than the normal bovine values of

32 (Belonje, 1978) and 34 (Coles, 1967). Because TPP was higher during the dry season, circulating albumin was also predictably greater (P < 0,01). Since circulating levels of albumin are considered a good indicator of nutritional status (Wilson and Hirst, 1977) and also of liver dysfunction (Doxey, 1971), it appeared that the wildebeest were not severely stressed in regard to nutrition or liver abnormalities. By comparison, TPP of adult Sable antelope in a suitable habitat was 65 g/l (Wilson and Hirst, 1977) and that of adult Alaskan moose, considered to be in average or better condition, was 75 g/l (Franzmann and LeResche, 1978). Furthermore, the normal range of the plasma albumin fraction is 40 - 60 % of TPP (Coles, 1967). Wildebeest contained 52,29 % albumin in their TPP, which was at the midpoint of this range.

9.3.4.2 Total and Ionised Calcium

The mean calcium level in all wildebeest plasma samples was 2,41 mmol/l ± 0,31 (range 1,16 - 3,02). This was within the range of the means reported for bovines, namely 2,32 mmol/l (Doxey, 1971) and 2,77 mmol/l (Belonje, 1978). Alaskan moose, considered to be in good to excellent condition, had a level of 2,60 mmol/l serum calcium (Franzmann and LeResche, 1978). There was no difference between wet and dry season levels of circulating calcium, neither did sex or age differences feature significantly ($P > 0,10$). In addition, I could find no meaningful relationship between total calcium and total protein ($r = 0,15$). This contrasted with studies on domestic animals where a decrease in TPP was found to influence the total calcium level (Coles, 1967). He nevertheless affirmed that TPP may have no relation to the amount of physiologically active (ionised) calcium present. Since excessive or deficient levels of circulating calcium (and TPP) have been associated with renal dysfunction and severe nutritional stress respectively (Coles, 1967), and neither condition was noted in this investigation, it seems reasonable to accept that the wildebeest's nutritional status was normal in regard to calcium.

The level of free and therefore physiologically active calcium in blood is about 50 % of the total calcium, the physiologically inert calcium being bound mostly to the albumin fraction of TPP (Cardielhac as quoted by Franzmann and LeResche, 1978). Free calcium is vital to neuromuscular function, cell membrane permeability and blood coagulation (Doxey, 1971). To calculate ionised calcium from total calcium, I used the formula :

$$\mathrm{Ca^{++} mmol/l} = \frac{720\ \mathrm{Ca_{total}} - \mathrm{TPP}}{12\ \mathrm{TPP} + 720} \qquad \text{(Louw, 1978, pers.comm.)}$$

$$\text{Thus}: \frac{720(2{,}41) - 69{,}65}{12\ \ (69{,}65) + 720} = 1{,}07 \text{ mmol/l}$$

which is 44,39 % of the total circulating calcium. Consequently, on average, 55,61 % of the total calcium in the wildebeest plasma samples was considered to be bound calcium. To establish whether a relationship existed between bound calcium and albumin, I computed the regression equation by the method of least squares. No linear relationship between these two parameters could be found on a seasonal or sexual or age basis. This was evident from the correlation coefficients which were 0,56 (wet season), 0,05 (dry season), 0,08 (bulls), 0,27 (cows), 0,53 (immatures) and 0,02 (adults). Consequently, predictions of albumin levels from bound calcium could not be made in the case of wildebeest plasma nor were they necessary as both determinations had been carried out.

9.3.4.3 Inorganic Phosphorus

Mean inorganic phosphorus present in wildebeest plasma was 1,47 mmol/l ± 0,51 (range 0,72 - 2,82). Normal bovine levels are 2,87 mmol/l for calves and 1,78 mmol/l for adults (Belonje, 1978), but immature and adult wildebeest values were 1,75 and 1,35 respectively. Thus wildebeest calves had only 61 % of the normal inorganic phosphorus in bovine plasma and adults only 76 %. Adult Sable antelope, which were considered to be deficient in circulating inorganic phosphorus had a level of 1,62 mmol/l, whilst those in a habitat with sufficient phosphorus in the soil had a level of 3,66 mmol/l (Wilson and Hirst, 1977). Adult Alaskan moose were considered to be in average to good condition when their blood level of inorganic phosphorus reached 1,68 (Franzmann and LeResche, 1978). It is therefore probable that wildebeest at Etosha may suffer from a marginal phosphorus deficiency. Deficiencies of this important nutritive element are common in southern Africa (Wilson and Hirst, 1977), including Etosha (Le Roux, 1977, pers.comm.). Moreover, water samples from Etosha revealed no phosphorus in rainwater pools, river water, boreholes or artesian wells and very low levels in fountains from which wildebeest prefer to drink (0,001 mmol/l; Section 7.3.10).

One of the major causes of hypophosphatemia is inadequate intake of this mineral and bovines appear to be especially susceptible (Coles, 1967). A feature of phosphorus deficiency is a low circulating level which may be accompanied by primary clinical symptoms, namely bone chewing (pica) and lameness (Coles, 1967). Neither of these symptoms was observed in wildebeest, but I have recorded bone chewing in Etosha's giraffe.

Because circulating phosphorus and ionised calcium levels vary reciprocally, to the extent that a fall in inorganic phosphorus may be accompanied by a rise in calcium following resorption of calcium from bone (Doxey, 1971), I computed a regression equation for inorganic phosphorus and ionised calcium in wildebeest plasma. No linear relationship was found ($r = 0,01$). This may have been because animals with low circulating levels of phosphorus have been known to show normal circulating calcium levels, even when clinical symptoms of phosphorus deficiency were evident (Coles, 1967).

Significant differences in circulating levels of inorganic phosphorus on a seasonal, sex and age basis were apparent. For example, wet season levels of this mineral were significantly higher than dry season levels ($P < 0,01$), cows had a higher level than bulls ($P < 0,05$) and immatures had a higher level than adults ($P < 0,01$). Seasonal differences may have been caused by area preferences, since wildebeest congregated on annual grassveld during the rainy season. Future research on nutritional status should consequently monitor soil and grass phosphorus in the wet season dispersal areas and dry season concentration areas of Etosha (Section 7.4.4). Differences related to sex have been found during lactation studies on domestic animals, when phosphorus loss may be as much as 1 g per litre of milk (Doxey, 1971). This high phosphorus demand would require that wildebeest cows forage from suitably nutritive pasture, and evidence that they chose the best grazing was found during a study of their activity patterns (Section 4.3.6). Higher levels of inorganic phosphorus due to bone growth were found to occur in young domestic calves (3,0 mmol/l) than in old cattle 1,61 mmol/l) (Doxey, 1971), which was similar to the findings of this study.

9.3.4.4 Cholesterol

Circulating levels of plasma cholesterol originate mostly from the liver (Coles, 1967) and the mean in wildebeest was 1,80 mmol/l ± 0,35 (range 1,10 - 3,04). This was 60 % of the normal domestic bovine values of 2,6 mmol/l (Doxey, 1971) and 63 % of 2,86 mmol/l ± 0,83 (Belonje, 1978). Low levels of cholesterol have been attributed to a low fat diet, anaemia, liver or thyroid dysfunction, or they could have been caused by stress resulting from capture or shooting (Coles, 1967). I will discuss this stress factor in my conclusions (Section 9.3.4.10). Since it is unlikely that anaemia or organ dysfunction were involved in Etosha wildebeest (Basson, 1979, pers.comm.), I examined the dietary fat levels which were obtained when analysing the grass (Section 7.3.2; Table 7.1).

The seasonal percentage fat in grass was low throughout the year, namely 2,59 at dormancy, 4,48 at sprouting and 3,62 at seeding. Consequently no hepatic lipidosis ("fatty liver") which results from a high fat level in the diet (Doxey, 1971) was observed during post mortem examinations (Section 10). In addition, no statistical differences in the circulating level of cholesterol were found to occur on either a seasonal or sex or age basis ($P > 0,10$). Furthermore, because the diet of domestic cattle in highly developed countries is supplemented by vegetable or animal fats (Maynard and Loosli, 1962) it is likely that the bovine blood cholesterol levels considered normal for domestic stock have been increased by supplementary feeds.

9.3.4.5 Non-Protein Nitrogenous substances (NPN)

Urea is the most important fraction of NPN, constituting about 50 % of the total and is the end product of protein metabolism (Doxey, 1971). The mean level of urea in wildebeest plasma was 6,57 mmol/l ± 1,86 which was above the normal bovine range of 1,0 - 4,48 mmol/l given by Belonje (1978). However, it fell within the range (1,99 - 6,64 mmol/l) considered normal for domestic cattle (Doxey, 1971), who states that values above 6,64 mmol/l should be regarded as significant for prognosis of nephritis, providing urinary and clinical symptoms are also significant.

In wildebeest there was significantly more circulating urea during the wet season ($\overline{x}$ = 8,06 mmol/l) than during the dry season ($\overline{x}$ = 5,78 mmol/l) at $P < 0,01$, but no differences were found between the sexes or in age groups ($P > 0,05$). Although the wet season levels of circulating urea were above the normal limit of 6,64 mmol/l (Doxey, 1971) the absence of significant pathological symptoms in kidneys and urine of shot wildebeest (Section 10) precluded the possibility of nephritis. Blood urea nitrogen (BUN) is increased by a dietary increase in protein (Coles, 1967) which was found to be very much higher in the wet season at Etosha (Section 7.3.2), possibly exceeding the levels which could be utilised by wildebeest (Section 7.4.4). The relatively high level of circulating urea during the dry season, when dietary crude protein was found to be below a critical level of 5 % $^{W}/_{W}$ DM (Section 7.4.3), was probably a result of the wildebeest's ability as a ruminant to recycle urea via the blood and the saliva (Maynard and Loosli, 1962). The significantly higher levels of crude protein which existed in wildebeest faeces compared to the feed during the dry season (Section 7.4.5) give additional support for this argument.

Similarly, urate levels in the plasma were significantly higher during the wet season than during the dry season ($P < 0,01$) with no sex or age differences occurring ($P > 0,50$).

These fractions of undetermined nitrogen were present at a low level of $\overline{x}$ = 0,05 mmol/1 ± 0,03 (range 0,01 - 0,15). Because a decreased level of BUN is not a significant indicator of disease (Coles, 1967) nor reliable for nutritional assessment (Franzmann and LeResche, 1978) the urates were disregarded for the purpose of this study.

9.3.4.6 Bile Pigments

The mean value of total bilirubin in wildebeest plasma was 2,78 mmol/1 ± 0,56 (range 1,9 - 4,5) which was below the mean of 3,42 mmol/1, but within the range of 0 - 8,55 mmol/1 given by Belonje (1978). There were no seasonal or age-sex differences ($P > 0,50$). Since total bilirubin levels increase only with severe hepatic dysfunction (Doxey, 1971), the results were of limited value. Furthermore, total bilirubin was not considered to be a good indicator of nutritional status in Alaskan moose (Franzmann and LeResche, 1978), although the bound fraction of bilirubin is associated with protein (Coles, 1967). Low levels of this excretory product of the liver appear to have no nutritional significance, since the normal range commences at zero (Belonje, 1978). Consequently I considered the total bilirubin levels in wildebeest plasma to be of little value as an indicator of condition, but rather as a criterion of linear pathology.

The conjugated levels of bilirubin were zero in 64 out of 66 samples of plasma. In two cases, an immature bull and an immature cow, 1,0 umol/l was present in the wet season. Belonje (1978) gives a mean value of 3,42 umol/l (range 0 - 6,84) for domestic calves. The wildebeest level of this bilirubin fraction, which is coupled to glucuronic acid in the liver, was also disregarded as an indicator of condition.

9.3.4.7 Alkaline Phosphatase

Alkaline phosphatase is associated with the deposition of phosphorus, calcium and protein during ossification of bony tissue (Maynard and Loosli, 1962). Therefore growing animals will predictably have higher circulating levels of this enzyme. In wildebeest the mean level was 99,24 Mu/ml ± 18,0 (range 18,0 - 370,0). Belonje (1978) gives a normal bovine level of 83,8 Mu/ml (range 33,4 - 440,3). A wide range of alkaline phosphatase levels in ruminants appears typical (Coles, 1967; Doxey, 1971). Although no sex differences in this enzyme were detectable ($P > 0,50$), wet season levels were significantly higher than dry season levels ($P < 0,01$). This may be due to greater availability of inorganic phosphorus during the wet season (Section 9.3.4.3). Similarly, immatures had higher circulating levels of alkaline phosphatase than adults ($P < 0,01$) which reflects greater phosphorus mobility during growth. However, no linear relationships were found between alkaline phosphatase and TPP (r = 0,28) and total calcium (r = 0,17) and inorganic phosphorus (r = 0,24). The normal levels of this enzyme in wildebeest also indicated that no serious osteosis or hepatitis was present (Coles, 1967).

9.3.4.8 Glutamic Oxalacetic Transaminase (GOT)

GOT (aspartate amino transferase) has its principal function intracellularly within muscle, the liver and intestines (Coles, 1967). Therefore an increase in circulating level of GOT reflects cellular necrosis in these tissues. GOT in wildebeest plasma averaged 161,26 mU/ml ± 37,05 (range 109 - > 300). The literature gives a wide range of normal GOT values for domestic cattle. For instance, Coles (1967) reports 438 ± 57 mU/ml and 900 mU/ml (range 560 - 1 650) from early investigations, while Doxey (1971) gives means of 180, 200 and 293 mU/ml, with a range of 90 - 340 mU/ml. The relatively low levels of circulating GOT in wildebeest plasma indicated no abnormal cellular damage in the organs concerned. There was more GOT in circulation during the wet season than during the dry season ($P < 0,01$) which may have been a result of the greater muscular stress caused by exertion in captured and shot animals. This stress was a feature of sampling during the wet season when wildebeest were difficult to approach. No differences in sex or age existed in regard to GOT ($P > 0{,}10$). I concluded that GOT, although not directly related to nutritional status, did indicate that vital digestive systems such as the intestines and liver were functioning normally in regard to enzymatic transformation of essential amino acids.

9.3.4.9 Iron

A mean iron level of 24,69 umol/l ± 6,88 (range 10,8 - 54,0) was present in wildebeest plasma. This was within the normal bovine range of 10,2 - 29,0 (Belonje, 1978) and compared favourably with the level of 16,11 umol/l in adult Sable antelope sampled from a suitable habitat (Wilson and Hirst, 1977). At Etosha there was no seasonal difference in wildebeest plasma iron ($P > 0{,}50$), neither was there a difference between sexes ($P > 0{,}10$). However, immatures had significantly less circulating iron than adults ($P < 0{,}01$). This may have been because of a higher growth rate in these animals. Nevertheless, the level in immatures ($\overline{x} = 20{,}65$ umol/l) was well within the normal bovine range. In addition, the major symptoms associated with iron deficiency, namely anaemia and a mottled liver (Doxey, 1971) were absent in all post mortem specimens. Iron was therefore not a factor limiting the normal nutritional level in wildebeest.

9.3.4.10 Stress Factors Affecting Blood Analyses

A feature of the statistical findings from wildebeest blood analyses was that although most of the blood parameters examined were normal, no linear relationship was found to exist between associated substances. For instance, there was no linear regression between protein or its major fraction, albumin. Neither was bound calcium meaningfully related to albumin. Similarly, tests between ionised calcium and inorganic phosphorus, as well as between alkaline phosphatase, TPP, total calcium and inorganic phosphorus all yielded low coefficients of determination. These somewhat disappointing results may have been due to stress factors involved in the capture and shooting of wildebeest for blood samples.

The effect of capture stress and shooting on blood chemistry of springbok has shown that several circulating parameters may be affected abnormally (Gericke *et al.*, 1978). In addition, it has been found that the levels of most blood parameters may be affected by any form of stress and this will in turn influence laboratory results (Coles, 1967; Doxey, 1971). Thus, although the blood analyses of wildebeest gave a fair reflection of the nutritional status of the animals, subtle differences and relationships were probably masked by the effect of capture and shooting stress.

9.3.5 Liver Status

The results of wildebeest liver analyses are given in Table 9.8 and compared against levels obtained in wild and domestic bovines. The small sample size did not warrant further statistical treatment. A feature of the results was that six out of nine of the minerals assayed were at levels varying from 10 - 78 % of those found in liver samples from domestic cattle and several wild ungulates. (Table 9.8 contains a list of the literature referred to.) These lower levels in Etosha's wildebeest may have been caused by excessive calcium in the soil and the resulting high alkalinity could have reduced the availability of some of these mineral elements, particularly copper and cobalt, to the growing plants (Louw, 1978, pers.comm.). The effect, however, must have been marginal as the animals did not exhibit overt signs of anaemia which is a typical consequence of a deficiency of these micro-elements.

9.3.5.1 Macro-elements

In contrast to blood calcium levels (Section 9.3.4.2) liver

Table 9.8 : Nutritional status of wildebeest at Etosha as reflected by liver analyses (1978 - 79)

Measurement	Liver constituent (umol/l)								
	Calcium	Phosphorus	Magnesium	Copper	Manganese	Zinc	Iron	Cobalt	Selenium
Wildebeest[x]									
Maximum	96	7 174	264	136	11,0	952	1300	0,14	0,48
Minimum	53	5 792	158	13	7,3	73	191	0,09	0,32
Mean	73	6 584	222	45	8,1	118	520	0,12	0,40
± SD	13	486	35	35	1,6	165	302	0,02	0,05
Bovine levels[xx]									
Maximum	1529	15 200	417	589	3,0	479	1521	-	60,00
Minimum	32	11 900	46	14	1,4	87	96	0,10	0,64
Mean	280	13 987	172	150	2,0	152	433	0,30	4,00
± SD	403	1 048	95	148	0,4	109	345	-	-
Wildebeest levels as percentage of bovine levels	26	47	129	30	405	78	120	40	10

[x] Present study; [xx] Sources : Doxey (1971)
Harthoorn and Turkstra (1976)
Wilson and Hirst (1977)
Onderstepoort Veterinary Research Institute Report 3373/3380 (1978)
Veterinary Diagnostic Laboratory, Windhoek, Reports 2118/11/78 and 2492/3/79
Atomic Energy Board Report 22/5 (1979)

calcium levels varied considerably, but not to the extent found in adult Sable antelope (32 - 1 529 umol/l; Wilson and Hirst, 1977). The lower calcium levels encountered in wildebeest liver should not be considered significant, since blood calcium was normal, reflecting the homeostasis of this principal cation in body fluids. Wildebeest liver phosphorus levels were consistently higher than blood phosphorus levels, but were only 47 % of the mean level found in other bovines. This strengthens my earlier supposition that inorganic phosphorus may be marginally deficient in the forage and water available to wildebeest at Etosha. Liver magnesium in wildebeest was 1,29 times higher than in adult Sable antelope (Wilson and Hirst, 1977); however the range in wildebeest was far smaller and well within the bovine range (Table 9.8).

9.3.5.2 Trace and Toxic Elements

Copper, manganese, zinc, iron and cobalt are indispensable metallic cations. Copper levels in wildebeest liver were only 30 % of other bovine levels, with the maximum value of 136 umol/l below the mean of 150 umol/l for bovines. It therefore appears as if a marginal copper deficiency may exist in wildebeest, although no clinical symptoms, which occur at levels of 8 - 11 umol/l in domestic cattle (Doxey, 1971) were evident. Primary copper deficiency manifests itself in anaemia, changes in pelage colour, and bone brittleness in young animals (Doxey, 1971).

Manganese was four times higher (8,1 umol/l) in wildebeest than in adult Sable antelope (Wilson and Hirst, 1977) but this was not considered excessive since levels of 50 - 125 umol/l are required to interfere with haemoglobin formation, and severe symptoms such as growth suppression are only apparent at levels of 1 250 - 2 000 umol/l (Garner, 1963).

Zinc and iron levels were within the normal bovine range, but cobalt was low and fractionally above the level of 0,1 umol/l which is associated with deficiency (Doxey, 1971). A typical clinical symptom of cobalt deficiency is anaemia (Doxey, 1971) but this was not evident in the case of wildebeest.

Selenium levels were only 10 % of the levels found in domestic cattle and consequently the minute amounts of this potentially toxic trace element could be ignored. In view of the absence of overt clinical signs of muscular dystrophy, there was sufficient selenium in the diet.

9.3.6 Haemocytology

Haemocytological examination was limited to gross microscopic scanning of peripheral blood smears and no haemocyte counts were undertaken. No overt morphological abnormalities in blood cells were seen and no anaemic condition was evident (Basson, 1979, pers.comm.). Furthermore, during the examination of 532 wildebeest carcases at Etosha for anthrax in the blood (Ebedes, 1976b) no overt haemocytic abnormalities were seen (Ebedes, 1978, pers.comm.). Thus, in the absence of more definitive haemocytic measurements, it appeared that the wildebeest's nutritional status was not detrimentally influenced by inadequacy of the trace element nutrition (Section 9.3.5).

9.4 SUMMARY

9.4.1

The nutritional status of Etosha's wildebeest was assessed using visual condition ratings, kidney fat, bone marrow and blood plasma as indicators of nutritional stress.

9.4.2

The visual physical ratings of a large sample (n = 3 898) showed that 78 % of the wildebeest were in good to excellent condition. Twenty-one percent were in fair condition and less than 1 % were classified as being in poor to very poor condition. At no stage of the three-year visual sampling period did the population appear to be nutritionally stressed.

9.4.3

Although kidney fat was an indicator of nutritional status, it was found that a number of variables such as age, growth, reproduction, as well as technique in determining the kidney fat index, could influence the results. Nevertheless, the small sample (n = 16) supported the visual condition ratings, confirming that Etosha's wildebeest were in a healthy, nutritional state.

9.4.4

Whilst no meaningful relationship was found between bone marrow fat and dry mass of marrow in the small sample of 20 animals, the majority (13) had a marrow fat level of more than 80 %. The remaining seven wildebeest had lower levels, probably caused by the stresses of rutting, pregnancy, lactation and, in the case of two starving calves, separation from the mother. Bone marrow fat appeared to be the most sensitive indicator for assessing whether severe nutritional stress was present. However, individual variation suggested that, like kidney fat, it be interpreted with caution.

9.4.5

The analysis of nine blood parameters confirmed that Etosha's wildebeest were at a normal nutritional level in most nutrients except inorganic phosphorus. There appeared to be a seasonally induced chronic shortage of this critical element in circulation. The wet season's level, although significantly higher than the dry season's level, was nevertheless still below the acceptable level for bovines. However, the absence of pica, the generally good nutritional condition and high reproductive rate in the wildebeest population suggest that, although a marginal deficiency of phosphorus may exist, it is not a serious limiting factor in the population dynamics. Significant and predictable variation in circulating levels of blood substances were found between seasons, bulls and cows, immatures and adults. Total circulating protein was significantly higher during the dry season than the wet season which does not reflect the seasonal dietary levels. This confirmed the earlier findings of the study on the effects of food selection and faecal composition. In addition, the relatively high level of circulating urea during the dry season supported the assumption that active urea recycling was occurring. Bilirubin analyses did not reveal any liver pathology.

9.4.6

Although a functional association exists between the majority of circulating nutrients, no linear relationship could be demonstrated between any of them. This may have been due to the stress factors involved during the capture and shooting of animals.

9.4.7

Liver analyses, like blood analyses, suggested that wildebeest may have ingested insufficient amounts of phosphorus. In addition, copper and cobalt may also have been marginally deficient although no clinical symptoms were evident to confirm this. Calcium, magnesium, manganese, zinc and iron were present in acceptable amounts, whilst the level of selenium was negligible but sufficient.

9.4.8

Gross haemocytological investigation did not reveal any cellular abnormalities in the blood which supported the findings that the trace element supply was adequate.

9.4.9

The overall findings of this investigation indicated that the nutritional status of wildebeest at Etosha was normal to good, but that one critical nutrient, namely inorganic phosphorus, was chronically but marginally deficient. Nevertheless, the nutritive level of wildebeest was sufficiently high to discount nutrition as being a limiting factor for the population.

Section 10

DISEASE AND PARASITES

10.1 INTRODUCTION

In this phase of the investigation my intention was to establish whether disease and parasites had contributed to the sharp decline in wildebeest numbers at Etosha. Veterinary aspects of wildlife management have sometimes been regarded as a specialist field by ecologists and are consequently viewed in isolation when identifying the factors which may limit or reduce populations. Thus, whilst some investigations of wildebeest reproduction and population ecology have excluded the disease/parasite factor (Attwell, 1977), others have drawn attention to the significant role it can play (Talbot and Talbot, 1963; Watson, 1967). For example, the disappearance of rinderpest virus from the Serengeti wildebeest at about the end of 1961 (Watson, 1967) resulted in a 263 % increase in the population over a 10-year period (Sinclair, 1973a).

I therefore enlisted the aid of veterinary specialists to make a study of the pathology and parasite loads existing seasonally in Etosha's wildebeest. In addition, I referred to the extensive veterinary investigation carried out by Ebedes (1976a, b) which reviewed the epizoötiology of anthrax *Bacillus anthracis* in large herbivores at Etosha.

10.2 METHODS

10.2.1 Carcases

During a three-year period (1976 - 78), field diagnosis of anthrax was based on the procedure established by Ebedes (1976a). Because the presence of lions at a carcase did not necessarily indicate death by predation, all such cases where the "kill" had not been witnessed, were examined microscopically for anthrax by taking bloodsmears. Only undecomposed carcases were suitable for field diagnosis of anthrax.

10.2.2 Immobilisation

A total of 60 wildebeest were immobilised on a seasonal basis during the period 1976 - 78. From these, ectoparasites were collected and where dermal lesions or apparent mange were present, skin scrapings were taken and preserved in 70 % ethanol for laboratory investigation.

10.2.3 Sampling by Shooting

In 1978 eight wildebeest were selectively shot at the height of the wet season (February) and similarly, eight were shot at the height of the dry season (November). Subsequent to these samplings, a further nine wildebeest were shot in February 1979 to provide additional veterinary material. These 25 animals were individually selected by veterinarians as being representative of the population and likely carriers of disease and parasites. The carcases were autopsied by a team of three veterinarians and organs, tissues, blood, urine and faeces were taken for detailed laboratory analyses.

10.3 RESULTS

10.3.1 Anthrax Diagnosis

The diagnosed level of anthrax is given for wildebeest and the other large herbivore species occurring on the grasslands of Etosha (Table 10.1). From the data collected it is clearly evident that wildebeest were severely decimated by anthrax, followed by zebra, springbok and gemsbok. No anthrax was diagnosed in red hartebeest and ostrich during this period but this may have been due to the small sample.

Table 10.1 : Incidence of anthrax in relation to total recorded mortality in wildebeest and other large herbivores at Etosha (1976 - 78)

Season	Species	Mortality					
		Anthrax positive	Anthrax negative	Other causes including predation	Cause unknown	Total positive & negative & other causes	Anthrax positive as percentage of total
Wet, hot season (Jan. to April)	Wildebeest	22	3	4	14	29	76
	Zebra	60	21	36	82	117	51
	Springbok	16	3	21	13	40	40
	Gemsbok	0	0	8	7	8	0
	Hartebeest	0	0	1	0	1	0
	Ostrich	0	0	4	4	4	0
Dry, cold season (March to Aug.)	Wildebeest	8	1	4	24	13	62
	Zebra	10	3	29	32	42	24
	Springbok	2	2	41	17	45	4
	Gemsbok	0	0	5	6	5	0
	Hartebeest	0	0	1	0	1	0
	Ostrich	0	0	10	3	10	0
Dry, hot season (Sept. to Dec.)	Wildebeest	11	2	11	23	24	46
	Zebra	11	0	17	45	28	39
	Springbok	6	1	24	23	31	19
	Gemsbok	2	0	6	12	8	25
	Hartebeest	0	0	1	3	1	0
	Ostrich	0	0	7	16	7	0
Total for three years	Wildebeest	41	6	19	61	66	62
	Zebra	81	24	82	159	187	43
	Springbok	24	6	86	53	116	21
	Gemsbok	2	0	19	25	21	10
	Hartebeest	0	0	3	3	3	0
	Ostrich	0	0	21	23	21	0

As can be expected the number of carcases found where the cause of death was unknown was high (48 % in wildebeest, 46 % in zebra, 31 % in springbok, 54 % in gemsbok, 50 % in red hartebeest and 52 % in ostrich; $\bar{x}$ = 47 %). This was due to the rapidity with which carcases decomposed or were scavenged at Etosha.

10.3.2 Other Infections and General Pathology

The pathologist's report (Basson 1979) has been summarised in Table 10.2. The findings indicate that the pathologically poor condition of seven of the 25 wildebeest examined could be related to increased parasitism and/or diseases such as infectious pustula vulva-vaginitis (IPV) (= infectious bovine rhinotracheitus) and brain lesions. This was regarded as being significant.

10.3.3 Endoparasites

The parasitologists' reports (Thomas, 1978; Biggs and Anthonissen, 1978, 1979) are summarised in Table 10.3. Their results show that all parasite burdens were very low if judged against standard criteria for herbivores.

Table 10.2 : Results of veterinary autopsy for pathological conditions in 25 wildebeest at Etosha (1978-79)
Summarised from Basson (1979)

Pathological condition	Level of infection (%) n = 25	Symptoms	Role as a decimating factor
Gedoelstiasis (primary vector: parasitic Diptera)	100	Lesions in rete mirabile and myocardium	A small percentage of population may die directly or indirectly
IPV (Virus causing infectious pustula vulva-vaginitis)	46 (11,5 moderate to prominent)	Intranuclear inclusions & metritis; brain & liver lesions	Secondary blastomycosis possible; also abortions & neo-natal mortality
Chlamydiosis (fungal)	4	Intestinal lymphoid hyperplasia (?)	Abortion & neo-natal mortality
Wesselsbron (virus strain akin to Rift Valley fever)	4	Liver lesions	Possible abortion & neo-natal mortality
Coccidiosis (protozoal)	34,6	Moderate enteric lesions & diarrhoea	Very pathogenic in unhygenic, closed habitat
Blastomycosis (suspected)	77	Small pulmonary & prominent lymph node lesions	Severe infection is fatal
Lungworm & bronchial worm (nematodes)	57,7 & 11,5 respectively	Pulmonary & bronchial lesions	Severe infection weakens but direct mortality is unknown
Crithidiasis (protozoal)	4	Visceral lesions & diarrhoea	Not significant (n/s)
Besnoitiosis (protozoal)	7,7	Localised epidermal cysts occasionally invading genitalia & upper gastro-intestinal tract	N/s

Table 10.2 (continued)

Pathological condition	Level of infection (%) n = 25	Symptoms	Role as a decimating factor
Sarcosporidosis (protozoal)	80,8	Cysts in muscle tissue	N/s
Nasal filariasis (helminth)	11,5	Nasal lesions	N/s
General parasites & viruses	42,3	Hepatic lesions	Very mild and n/s
Calcareous cystitis, renal calculi & pyelitis (causative factors: brackish water & plants?)	23	Severest lesions occur in dry season	Insignificant mortality possible

Table 10.3 : Endoparasite levels in 25 wildebeest sampled on a seasonal basis at Etosha (1978 - 79)

Endoparasite	Degree of infestation	Role as a decimating factor
[*] *Theileria* sp. or *Cytauxzoön* sp.: Protozoa (peripheral blood smears)	Negative to very low level	Not significant (n/s); regarded as a carrier status only
Nematode eggs (faecal counts)	Negative to 1 300 eggs.g^{-1}	N/s
Coccidia oöcysts: Protozoa (faecal counts)	[**] Negative to 13 100 eggs.g^{-1}	N/s
Haemonchus spp.: nematode (estimates of total intestinal burdens based on 1:10 aliquots)	Negative to 1 260	N/s
Agriostomum spp.: nematode (estimates of total intestinal burdens based on 1:10 aliquots)	Negative to 40	N/s
Strongyloides (?) spp.: nematode (estimates of total intestinal burdens based on 1:50 aliquots)	Negative to 2 750	N/s
Trichostrongylus (?) spp.: nematode (estimates of total intestinal burdens based on 1:50 aliquots	Negative to 150	N/s
Cestodes: platyhelminth (total intestinal counts of adults and larvae)	Negative to 8	N/s
Protostrongylus spp. and *Dictyocaulus* (?) spp. nematode (pulmonary counts)	Negative to 9	N/s

[*] Identification by Thomas (1978); all other identifications by Biggs & Anthonissen (1978, 1979)

[**] Nematode egg counts of this order are seldom associated with clinical problems

10.3.4 Ectoparasites

The reports of the parasitologists (Biggs and Anthonissen, 1978, 1979) are summarised in Table 10.4. Tick and lice burdens were exceptionally low. In spite of regular *Gedoelstia* pathology (Section 10.3.2), the loads of this dipteran larva were regarded as low to typical and the parasite-host relationship appeared stable. Nevertheless, the possibility of mortality in calves as a result of gedoelstiasis does exist.

10.4 DISCUSSION

10.4.1 Anthrax

The viable nature and ecology of anthrax have been adequately dealt with by Van Ness (1971) and Ebedes (1976b). At Etosha, soils in the areas inhabited by wildebeest are highly alkaline, thereby providing conditions under which anthrax bacilli flourish. Furthermore, the creation of numerous gravel pits for road building in Etosha boosted the disease's incidence by creating favourable incubator areas for sporulation. Ebedes (1976b) confirmed that the manner in which anthrax could be transmitted, namely, by infected carcases, faeces,

Table 10.4 : Ectoparasite levels in 25 wildebeest sampled on a seasonal basis at Etosha (1978 - 79). Summarised from Biggs and Anthonissen (1978, 1979)

Ectoparasite	Degree of infestation	Role as a decimating factor
Lice[*] (Whole skin washings/ scrubbings over 150 u sieve)	Nil to 23	Not significant (n/s)
Ticks[**] (Retrieval as for lice)	Nil to 11	N/s
Gedoelstia larvae (Total counts in nasal, sinus & cranial cavities)	Nil to 202	Calf mortality possible
Mites (Scrapings of skin lesions; pinna & ear canal examinations)	Nil	-

[*] *Anopleura* and *Ischnocera* present

[**] *Hyalomma truncatum*
Rhipicephalus eversti mimeticus

predators, scavengers, birds and insects, as well as by water and wind, made it practically impossible to eliminate the disease in an area the size of Etosha. He also related the greatly increased incidence of anthrax at Etosha since 1966 to the emergence of over-utilised grazing areas. These "slum areas" (Ebedes, 1976a) were created by the construction of drinking troughs in the areas previously occupied by migrant herds in the rainy season only.

The findings of Ebedes (1976a, b) were supported by my observations during this five-year investigation. In addition, I am of the opinion that anthrax has resulted in an ideal situation in which predators and scavengers can increase to an unnatural level (Section 11). My supposition is partly derived from the high incidence of anthrax in relation to recorded mortality (Table 10.1), where it is apparent that a surplus of meat from carcases would be available. When it is considered that anthrax-infected carcases were especially abundant during the wet season, a period in which predators would normally experience greater difficulty in obtaining food (Schaller, 1972; Smuts, 1975, 1978c), the advantage to lions and hyaenas is obvious. The combination of anthrax and increased predation pressure has in turn been reflected in declining herbivore populations, notably wildebeest and zebra. The impact of anthrax on the reproductive component of the wildebeest population should also be considered. For example, the majority of wildebeest cows died of anthrax during the wet season when they were nearing full term pregnancy or had recently calved. This resulted in "double deaths" and may have contributed to a high antenatal and neo-natal mortality (Section 12.3) since milk-dependent calves are suckled only by their mother and are not fostered by other cows. There was no significant difference in mortality of the sexes in the sample collected by Ebedes (1976b) : 308 bulls : 303 cows ($P > 0,80$). In the present study the sample reflected a more distorted sex ratio of 24 bulls : 15 cows which was not significant at $P > 0,02$. This may have been due to the much smaller sample size.

It appeared that wildebeest were more susceptible than zebra to anthrax (Table 10.1) because the total number of anthrax - positive carcases located in relation to the total population was 1,93 times higher in the case of wildebeest. Ebedes (1976b) mentioned that possibly 50 % of all anthrax-infected carcases were located, but I am of the opinion that in wildebeest a much lower percentage was located. I base this on the fact that 48 % of my sample was made up of dehydrated or decomposed carcases from which no positive field diagnosis was possible.

Furthermore, a predated carcass was seldom found in a relatively intact, mummified state which characterised an anthrax epidemic, when more meat was made available to scavengers than could be utilised. None of these frequently occurring dried-out carcases or remains could be positively diagnosed in the field. Moreover, while herbivores were fatally affected by anthrax, no records of predators or scavengers dying of the disease were obtained during a seven-year investigation by Ebedes (1976b) or during the present study. Consequently, carnivores fed freely from anthrax-infected carcases, or drank from infected water, thereby gaining advantageously over the susceptible herbivore populations.

Thus I consider anthrax to be a primary and major factor in the decline of wildebeest at Etosha. The data in support of this are quantifiably demonstrable from both Ebedes'(1976a, b) findings and my results, namely, that in our respective samples 74 % and 62 % of all diagnosed deaths in wildebeest were positive for anthrax. Other herbivores, especially zebra, appeared to be similarly affected and this was reflected in their declining numbers (Section 8, Table 8.1).

10.4.2 Other Pathological Conditions and Parasites

The autopsy findings indicated that two age classes especially showed levels of viral infection and/or parasitism which could be considered potentially fatal (Basson, 1979, pers.comm.). These were the very young calves (< 2 months) in which disease, notably IPV, resulted in prominent brain lesions and the 1 - 2 year old immatures which exhibited widespread lesions from migrating *Gedoelstia* larvae. In comparison, the older, weaning calves (2 - 9 months) and wildebeest older than two years were noticeably less prone to these conditions. These findings dovetail well with my surmise that there was a high mortality of neo-natal calves, which, because it could not be quantitatively determined, has been included in my theoretical population model as a reduced birthrate in adult cows, namely 0,35 (Section 12, Table 12.5). Similarly, the pathology of 1 - 2 year old wildebeest was well correlated to my field counts where there was a greater decline in the number of calves achieving immaturity (8 % decrease) than in the number of immatures achieving sub-adulthood (4 % decrease) as is shown in Section 12, Table 12.3.

The autopsy findings also confirmed a high incidence of *Gedoelstia* larvae, and the burden carried by young calves pointed to the possibility of occasional deaths in young animals as a result of gedoelstiasis. However, this ectoparasite was not present in abnormally high levels in Etosha's wildebeest. The remaining parasite loads, especially ectoparasites, were exceptionally low in all specimens examined and were regarded as having no significant effect on the population's mortality.

10.5 SUMMARY

10.5.1

An investigation was undertaken to establish whether the declining wildebeest numbers at Etosha could be related to veterinary causes. This was achieved by monitoring a total of 127 wildebeest carcases and 337 carcases of Burchell's zebra, gemsbok, springbok, red hartebeest and ostrich over a period of three years. In the same period a total of 60 immobilised wildebeest were visually examined for external parasites and peripheral blood smears were made for blood parasites. In addition, 25 wildebeest were selectively sampled for detailed pathological and parasitological investigation.

10.5.2

Fresh carcass diagnoses yielded blood smears which were positive for anthrax *Bacillus anthracis* in 62 % of wildebeest, 43 % of zebra, 21 % of springbok, 10 % of gemsbok and were anthrax-negative in hartebeest and ostrich. Anthrax mortality reached a predictable peak in wildebeest, zebra and springbok during the rainy season when 76 %, 51 % and 40 % of anthrax deaths occurred in these species respectively.

10.5.3

Pathology showed that gedoelstiasis caused by parasitic dipteran larvae and viral infectious pustula vulva-vaginitis (IPV) were prominent. *Gedoelstia* infestations were responsible for lesions in the rete mirabile and myocardium of calves and 1 - 2 year old wildebeest. IPV manifested itself predominantly as metritis in adult cows and brain lesions in young calves. Both these conditions could be fatal in neo-natal calves. Gedoelstiasis could also be fatal in immatures and IPV could result in abortions. Wesselsbron virus disease and fungal conditions such as chlamydiosis and suspected blastomycosis were present in 4 - 11 % of the autopsied wildebeest.

10.5.4

The low endoparasite profile in wildebeest was regarded as an insignificant factor for limiting the population. Similarly, the ectoparasite burden was exceptionally low, except for *Gedoelstia* larval counts which approached typical herbivore levels.

10.5.5

The special conditions existing in wildebeest habitat at Etosha favoured anthrax viability and the disease was regarded as having become endemic with epidemics occurring during the wet season. An abundance of anthrax-infected carcases during the wet season probably resulted in increased predator-scavenger populations. Carnivores were apparently not fatally affected by anthrax. There was no significant sex link in wildebeest mortality from anthrax but the deaths of reproductive cows naturally also resulted in the loss of foetuses and neo-natal calves.

10.5.6

Reviewing the disease and parasite pressure on wildebeest at Etosha, it is evident that anthrax was a primary and major factor in the reduction of the population up to the present time and that it will not be possible to eliminate it in the foreseeable future. Other diseases and parasites were found to be insignificant in comparison to anthrax, but gedoelstiasis and IPV are potentially fatal conditions which, if they were to become severe, could result in increased mortality.

Section 11

PREDATORS AND SCAVENGERS

11.1 INTRODUCTION

During the investigation of factors which may have resulted in the decline of wildebeest numbers at Etosha, I also considered the role of predators and scavengers. Predation of herbivores and the presence of scavengers are natural phenomena and are desirable in any large area set aside for conservation of wild animals (Estes, 1967; Hirst, 1969; Pienaar, 1969; Kruuk, 1972; Schaller, 1972). However, because all terrestrial systems have been influenced by man, it is possible that this natural equilibrium can become unstable, resulting in an abnormal predator-prey ratio (Smuts, 1975, 1976, 1978a, b, c). I consequently examined the numbers, age-sex ratios, group size, prey preferences and estimated the food intake of large predators and scavengers at Etosha. These data were used to establish whether the predator-prey ratio was within acceptable limits when compared to other African conservation areas.

At Etosha, information on large predators and scavengers is limited to the lion and cheetah, with a few records of observed kills by spotted hyaena, leopard, wild dog and black-backed jackal. No other relevant data exist for these species, apart from casual sightings. I have therefore been obliged to refer to subjective observations made by staff and tourists when dealing with the lesser known species. In addition, since virtually nothing is known about the predator-prey relationship in the bush and woodlands of Etosha, I have dealt only with the situation relating to the plains, which are the major habitat of wildebeest.

11.2 METHODS

11.2.1 Number of Predators, Age-Sex Ratios and Group Size

To estimate the predator and scavenger populations in the areas inhabited by wildebeest and other large herbivores sharing the grasslands, I relied on counts made by nature conservators, research workers and my ground and aerial observations during the period 1974 - 78. Data on age-sex ratios and group size were recorded on punch cards and subsequently coded on to Fortran sheets for sorting. Additional information was obtained from questionnaires which were handed out to tourists.

11.2.2 Preferred Prey Species

Prey preferences could be obtained for lion, cheetah and spotted hyaena and were calculated from the formula used by Pienaar (1969), Rudnai (1974) and Smuts (1975) :

$$PR = \frac{F}{A}$$

where PR = preference rating

F = relative frequency with which a particular prey species is killed (%)

A = relative abundance of the prey species (%)

As pointed out by Schaller (1972), the term "preference" is misleading in that a kill also signifies the prey's availability and vulnerability. I have accordingly considered the preference rating to be an expression of these two factors as well.

11.2.3 Estimated Food Intake per Predator Species

With no data available from Etosha, I referred to the comprehensive investigations of Wright (1960), Kruuk (1972), Schaller (1972), Eloff (1973b) and Bryden (1976). From their data it was possible to extrapolate the estimated amount of food required annually by lion, cheetah and spotted hyaena on the plains of Etosha. Although the preferred prey species of large predators differs greatly between various areas in Africa (Bourliere, 1963), the amount of food required by large carnivores is probably consistent at 4 - 6 % of their body mass per day (Kruuk, 1972; Schaller, 1972; Smuts, 1975). Consequently, by applying a mean daily food intake of 5 % of body mass I was able to estimate the amount of food required by the major predators and scavengers at Etosha with a reasonable degree of confidence and then balance this requirement against the live mass of available prey.

11.3 RESULTS AND DISCUSSION

11.3.1 Estimated Predator-Scavenger Populations and Their Composition

11.3.1.1 Lion

The dry season pride areas of resident lion and ranging nomadic groups (as defined by Schaller, 1972) which inhabited the Etosha plains during the period 1974 - 78 are shown in Fig. 11.1. Pride areas were fairly distinct during the dry season when availability of drinking water restricted the movements of predators and most prey species. In all,

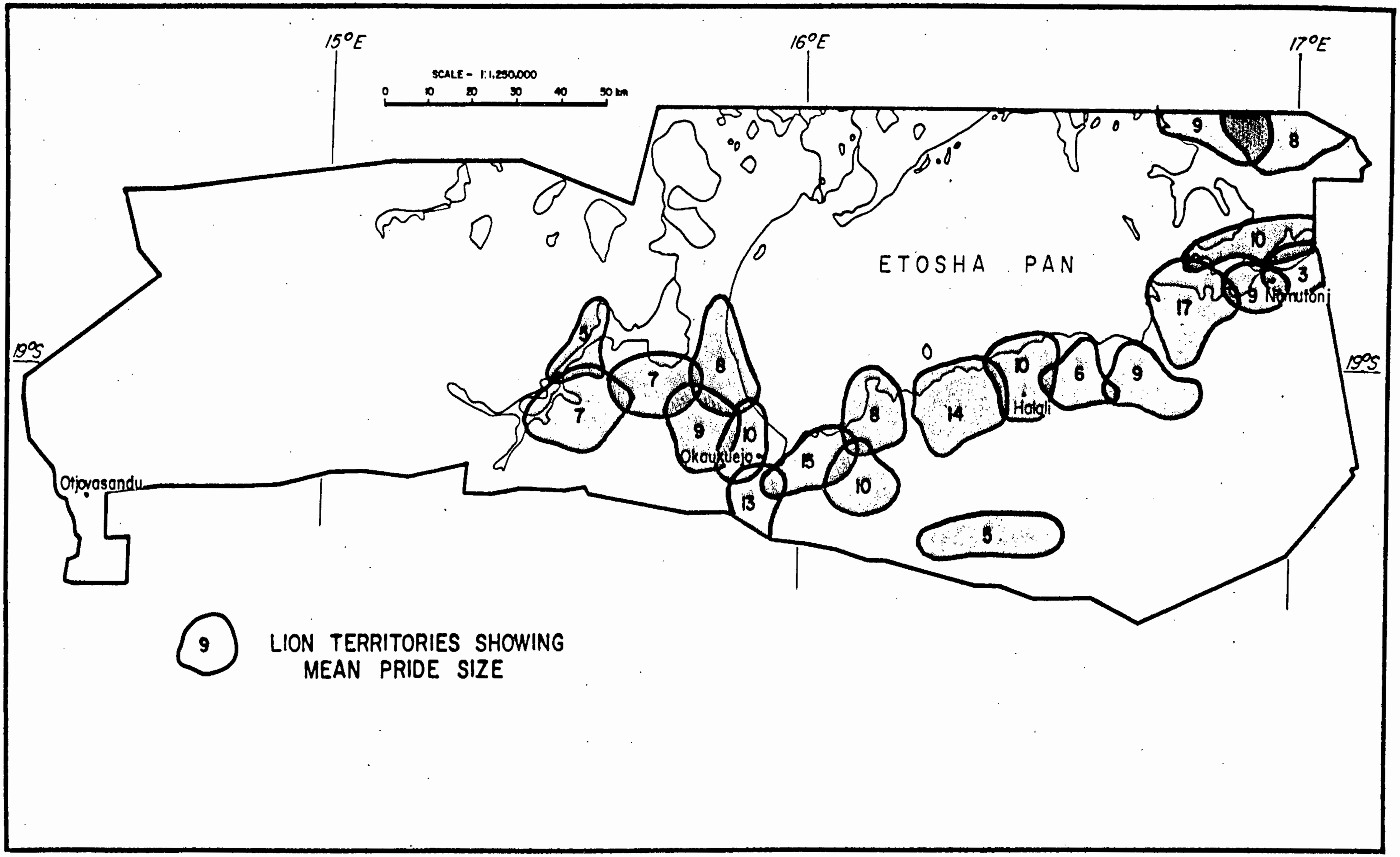

Fig. 11.1 : Dry season pride areas and ranges of 21 known lion groups on Etosha's grasslands (1974 - 78).

there were 21 known areas on the Etosha plains which were inhabited by resident prides or nomadic groups. Pride areas became obscure during the wet season when distribution of prey changed and wet conditions prevented vehicles from leaving the roads. The mean pride or group size in each area or range was calculated from observations during the five-year period (n = 356 observations on 2 562 lions). The overall mean pride/group size was 7,2 (range 2 - 30, SD ± 4,53), with a yearly mean of 285 individuals present. I was able to age and sex 565 lion. Adult sex ratio was 1 male : 1,03 female (n = 354) which was not disparate at P > 0,70. Immature lion (0 - 3 years) made up 37 % of my sightings.

By comparison, Schaller (1972) found that Serengeti lion pride size was 15 (range 4 - 37) and nomadic group size was 2,8 (range 2 - 13) giving an overall average of 4 lion in prides and groups. Their sex ratio was 1 male : 0,92 female (P > 0,50), whilst 43 % of the lion on the Serengeti plains were sub-adult (0 - 4 years). Thus the mean pride/group size in Etosha was larger than in Serengeti, although the age-sex ratios were similar. Etosha's pride/group size of 7,2 is also greater than the figure of 4 - 5 given for Zambia by Mitchell *et al.* (1965), but is more in keeping with the group size of 6 reported in East Africa by Wright (1960). In contrast, Smuts (1975) reported an average of 11,8 lion per pride/group in the central Kruger Park.

My figure of 285 lion inhabiting the Etosha plains is likely to be an underestimate since only limited observations were available from some of the areas and lion are usually undercounted from the ground or by aircraft (Schaller, 1972; Smuts, 1975). Because no correction factor for undercounting bias is known for free-ranging lion, I assumed that approximately 70 % of the total population were seen by ground counts. Consequently I applied an arbitrary correction factor of 1,4 to the average count of 285 lion, which provided a theoretical total of 400 lion that may have been present on the plains of Etosha during this study. I subsequently used a range of 285 - 400 lion when calculating predator density and food intake, since it is likely that the actual number of lion present fell within these minimum and maximum figures.

The plains of Etosha cover 8,1 % of the total area, namely 1 793 km^2 (Le Roux, 1977). Applying my estimates of between 285 and 400 lion, the density is one lion/ 4,5 - 6,3 km^2. These first approximations are well within the range of lion densities found elsewhere in Africa. For example, one lion/2,6 km^2 in Manyara Park, one lion/3,7 km^2 in Ngorongoro Crater, one lion/4,6 km^2 in Nairobi Park

(Schaller, 1972) and one lion/7,9 km^2 in Kruger Park (Smuts, 1975). My estimates of the lion population on Etosha's plains therefore appear to be of the right order of magnitude.

11.3.1.2 Cheetah

The records show that, on average, there were 70 - 80 cheetah inhabiting Etosha's plains between 1974 - 78. Allowing for double-counting as well as for undercounting, I consider that a population figure of 50 - 100 cheetah is realistic. These estimates give a density of one cheetah/18 - 36 km^2. In comparison, Nairobi Park supported one cheetah/4,42 km^2 (McLaughlin, 1970), while Kruger Park had one cheetah/72 km^2 (Pienaar, 1969) and Serengeti's density was one cheetah/102 - 107 km^2 (Schaller, 1972). Group size at Etosha varied from 2 - 5. The most adults reported together were three, whilst groups of 4 - 5 animals were females with up to four cubs.

11.3.1.3 Spotted Hyaena

The number of spotted hyaena, hereafter referred to as hyaena, inhabiting the plains of Etosha is unknown and I have used the ratio of hyaena : lion from other areas to estimate a figure. Nonetheless, my casual observations and those of other observers at Etosha indicate that the hyaena population is substantial and my initial estimates can therefore be regarded as realistic. The ratio of hyaena : lion in Ngorongoro Crater is 6,1 : 1 and in Serengeti it is 1,25 - 1,50 : 1 (Kruuk, 1972; Schaller, 1972). In the Kruger Park it is 2,73 : 1 (Smuts, 1975), while in the adjoining Timbavati Nature Reserve it approximates 1 : 1 (Bearder, 1975). Thus it appears that in large, relatively natural conservation areas there are at least as many hyaena as lion and often more. Consequently, I estimated the hyaena population on Etosha's plains to be the same as for lion, namely 285 - 400. These figures are probably conservative.

Hyaena packs of more than three adults were frequently seen at Etosha. The largest pack encountered in daytime was 12 and at night a pack of 23 was observed. By comparison, up to 25 hyaena in a pack were recorded at Serengeti - Ngorongoro (Kruuk, 1972). Since pack information indicates either active hunting or patrolling of territory boundaries (the latter in itself indicates a fairly dense hyaena population according to Kruuk, 1972), it appears that Etosha's hyaena hunt frequently. The records at Etosha show that healthy, adult zebra, wildebeest, kudu and springbok have been successfully hunted and killed by hyaena packs. This in turn indicates that at certain times of the year scavenging from lion kills is insufficient to meet the food demand of hyaena.

11.3.1.4 Other Predators and Scavengers

No information exists on the numbers of leopard and brown hyaena at Etosha, while in the case of wild dog it is virtually certain that they did not inhabit the plains during 1974 - 78. I estimate that there may be 1 000 - 2 000 black-backed jackal on the plains, giving a density of 1 jackal/0,9 - 1,8 km^2. Up to 52 jackal have been recorded at a zebra carcass and groups approximating 30 are frequently encountered at anthrax carcases. There is no doubt that the jackal population is high and my estimates may well be conservative.

I have not considered vultures and other avian carrion eaters in my estimates of predator-scavenger biomass, since they are not necessarily resident on the plains. The omittance of these other mammalian and avian species lends conservative bias to the estimated predator-scavenger biomass and consequently to the predator : prey ratios. This bias may, however, be offset to an extent by the fact that the major carnivores I have considered also predate and scavenge species other than the large herbivores included in my estimates.

11.3.2 Preferred Prey Species

The prey preferences of lion, cheetah and hyaena are given in Table 11.1. Lion showed the greatest preference for gemsbok, followed by wildebeest, zebra, ostrich and springbok. In other areas where gemsbok are common, for example the Kalahari Park, they are frequently taken by lion (Eloff, 1964). However, prey preference is largely dictated by availability of species. For instance buffalo made up 9 % of the lion's diet in Kruger Park (Pienaar, 1969), 15 % in Serengeti (Schaller, 1972; Sinclair, 1977), but constituted 62 % of the prey species at Manyara Park, an area where buffalo outnumbered all other prey species (Makacha and Schaller, 1969). Likewise at Kruger Park, where impala were the most plentiful prey species, they constituted the highest frequency (31,3 %) of food for lion (Smuts, 1978b).

I suspect that the preference shown for gemsbok at Etosha may be due to the establishment of artificial drinking places where gemsbok, a species which is relatively independent of drinking water, are found in the dry season. Consequently, these boreholes especially Leeubron, Adamax, Gemsbokvlakte and Gaseb (Fig. 2.1) support large groups of lion. Under natural (waterless) conditions, no lion could be resident in these areas of Etosha during the eight months of dry

Table 11.1 : Preferred prey species of lion, cheetah and spotted hyaena on the grasslands of Etosha (1974 - 78)

Predator	Prey species	No. of kills recorded	Relative kill frequency (%)	Relative abundance of prey (%)	Prey preference rating*
Lion	Wildebeest	21	19,1	6,4	2,98
	Zebra	67	60,9	24,1	2,53
	Springbok	12	10,9	65,0	0,17
	Gemsbok	9	8,2	2,3	3,57
	Red hartebeest	0	0,0	0,2	0,00
	Ostrich	1	0,9	2,0	0,45
Cheetah	Wildebeest	2	3,2	6,4	0,50
	Zebra	0	0,0	24,1	0,00
	Springbok	61	96,8	65,0	1,49
	Gemsbok	0	0,0	2,3	0,00
	Red hartebeest	0	0,0	0,2	0,00
	Ostrich	0	0,0	2,0	0,00
Spotted hyaena	Wildebeest	2	22,2	6,4	3,47
	Zebra	5	55,6	24,1	2,31
	Springbok	2	22,2	65,0	0,34
	Gemsbok	0	0,0	2,3	0,00
	Red hartebeest	0	0,0	0,2	0,00
	Ostrich	0	0,0	2,0	0,00

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

season. A similar situation was found to exist in Wankie Park, where gemsbok and eland suffered disease and predation stresses beyond their adaptive capabilities (Davison and Davison, 1968).

Wildebeest are marginally preferred to zebra by hunting lion at Etosha (preference rating = 2,98 compared to 2,53). In Kruger Park the PR for wildebeest ranged from 2,21 - 4,35, while that for zebra was 1,43 - 2,37, making wildebeest preferred above zebra, on a yearly basis, for a period of 20 years (Smuts, 1975). The PR values were of a similar magnitude in Nairobi Park, where wildebeest PR = 1,83 - 4,20 and zebra PR = 0,81 - 1,98 (Rudnai, 1974). Wildebeest were also preferred above zebra by lion in the Timbavati Reserve, Eastern Transvaal (Hirst, 1969).

Predictably, cheetah prey mainly on springbok at Etosha, although wildebeest, especially calves, may be taken. Wildebeest appear to head the list of prey preferences of hyaena at Etosha, ranking above zebra and springbok. The small sample size (n = 9 kills) may, however, have biased the findings.

11.3.3 Live Mass of Food Required Annually

Applying a mean daily food intake of 5 % of body mass, I estimated the food requirement in Etosha's large, plains-dwelling carnivores (Table 11.2). As mentioned previously, leopard, wild dog, brown hyaena, jackal and vultures were omitted from these estimates. Furthermore, I presumed that 37 % of the lion population was immature, basing this on field observations at Etosha. For cheetah, 32 % of the population was taken to be immature (Schaller, 1972) and in the case of hyaena this figure was 25 % (Kruuk, 1972). Live mass of the three carnivore species was based on the means recorded by Kruuk (1972) and Schaller (1972).

Because lion and cheetah, on average, leave 33 % and 35 % of a carcass uneaten respectively (Schaller, 1972), I have estimated the total food actually killed to be accordingly higher. In the case of hyaena, my assumption was that almost 100 % of a carcass was consumed (Kruuk, 1972; personal observation).

The estimates result in a total food requirement plus uneaten residues of approximately 1 - 1,5 million kilogram prey annually. I wish to reiterate that these figures should be considered initial approximations, since my calculations are based on several unproven assumptions.

Table 11.2 : Estimated amount of prey killed and carcases scavenged annually by lion, cheetah and spotted hyaena on the grasslands of Etosha (1974 - 78)

Predator/scavenger species	Population		Mean live mass (kg)		Total live mass (kg)		Total annual food requirement (kg)
	Adult	Immature	Adult	Immature	Adult	Immature	
Lion	180-252	105-148	145	73	26 100 - 37 296	7 665 - 10 804	819 561 - 1 167 507
Cheetah	33-68	15-32	60	30	1 980 - 4 020	510 - 990	61 348 - 123 435
Spotted hyaena	215-300	70-100	52	26	11 180 - 15 600	1 820 - 2 600	189 800 - 265 720
Totals	-	-	-	-	39 260 - 56 916	9 995 - 14 394	1 070 709 - 1 556 662

11.3.4 Predator - Prey Live Mass Ratios

Estimates of the ratios of predator to prey on the Etosha plains are given in Table 11.3. To calculate these ratios I used the estimated maximum and minimum total live mass of the three major predators, namely lion, cheetah and hyaena as derived in Table 11.2. This range of predator live mass was related to the live mass of wildebeest and the other five major herbivore species which inhabit the plains. In estimating the live mass of prey, I took into account the contribution made to each species' population by the different age and sex classes, using the appropriate body mass of each age-sex class. These data were obtained from Table 5.1 in the case of wildebeest and from Appendices 26 to 31 in the cases of zebra, springbok, gemsbok, hartebeest and ostrich. Furthermore, I used the mean population of each prey species during the period 1974 - 78 to correspond with the mean predator populations for the same period.

Thereby, the total predator - scavenger live mass was estimated to lie between 49 255 and 71 310 kg and the total live mass of prey was estimated at 5 151 013 kg, as shown in Table 11.3. This gives a minimum predator : prey ratio of 1 : 72 and a maximum of 1 : 105. A comparison of these ratios to those found elsewhere in Africa is made in Table 11.4. Etosha appears to have a greater proportion

Table 11.3 : Estimated mean predator-prey live mass ratios on the grasslands of Etosha (1974 - 78)

Predator species	Predator live mass (kg)	Prey species	Prey live mass (kg)	Predator-prey ratios
Lion	33 765 - 48 100	Burchell's zebra	3 564 112	1 : 72 to 1 : 105
Cheetah	2 490 - 5 010	Wildebeest	521 250	
Spotted hyaena	13 000 - 18 200	Springbok	700 681	
		Gemsbok	261 295	
		Red hartebeest	18 160	
		Ostrich	85 515	
Total predator live mass	49 255 - 71 310	Total prey live mass	5 151 013	

Table 11.4 : Comparison of predator-prey ratios on the grasslands of Etosha with other areas of Africa

Area	Lion : Prey ratio & Predator : Prey ratio	Source
Albert Park	1 : 360[x]	Bourliere (1965)
Kagera Park	1 : 300[x]	"
Tarangire Game Reserve	1 : 292[x]	Lamprey (1964)
Ngorongoro Crater	1 : 260[x]	"
	1 : 100[xx]	Schaller (1972)
Serengeti Park	1 : 250 - 300[xx]	"
Manyara Park	1 : 174[xx]	"
Nairobi Park	1 : 100[xx]	"
Kruger Park	1 : 100[xx]	Pienaar (1969)
	1 : 100 - 116[x]	Smuts (1976)
	1 : 57 - 149[x]	Smuts (1978c)
Etosha Park	1 : 107 - 153[x]	Present study
	1 : 72 - 105[xx]	"

[x] Lion : prey ratio

[xx] Predator : prey ratio

of lion to prey than most other conservation areas for which data are available. It must, however, be remembered that Schaller's (1972) ratios for Serengeti include all major predators, whereas the other sources refer specifically to lion : prey ratios. For this reason I have presented Etosha's ratios in both ways.

In central Kruger Park, which has similar ratios to Etosha, a total of 335 lions and 297 hyaena, representing 63 % and 80 % of the numbers in one area, were cropped between 1974 - 77 (Smuts, 1975, 1978c). Despite this high rate of predator control, lion regained 90 % of their former level within 17 months while hyaena were slow to recolonise (Smuts, 1978a). Therefore it seems that the question of direct predator control at Etosha would have to be approached with caution in view of the limited success achieved elsewhere.

The 1 - 1,5 million kilogram prey removed annually (Table 11.2) is 21 - 30 % of the estimated herbivore live mass of 5 million kilogram (Table 11.3). This rate of removal by predators is two to three times that in the Serengeti where 9 - 10 % of the prey biomass is taken by predators (Schaller, 1972), whose findings indicated a dearth of large carnivores. The relative paucity of prey at Etosha can be illustrated by the prey biomass which is estimated at 2 873 kg/km^2 compared to 20 712 kg prey/km^2 in Serengeti (Schaller, 1972). Moreover, the lion biomass at Etosha is estimated between 18,8 - 26,8 kg/km^2 which is higher than the range of 13,6 - 20,5 kg/km^2 found in four areas of the Kruger Park (Smuts, 1978c) despite the fact that he applied a mean adult body mass of 158 kg for lion which is 9 % higher than the figure of 145 kg which I used.

11.3.5 Combined Effect of Predation and Disease

At Etosha, a portion of the carnivores' food is provided by diseased animals which die of anthrax (Section 10.3.1). Thus, during an anthrax epidemic, lion and hyaena are not required to hunt but can live off the abundant supply of diseased meat without suffering any apparent clinical ill-effects. Nevertheless, lion may continue to hunt in the presence of diseased carcases and there are records of Etosha lion ignoring several zebra which had died of anthrax, to commence a successful hunt on healthy zebra in the vicinity. Under these circumstances the live mass of herbivores removed by the combined effect of predation and disease would be higher than the estimates of 1 - 1,5 million kilogram obtained in Table 11.2. Even if this were not the case, my estimates can still be considered conservative because, during an anthrax epidemic, more herbivores die than can be eaten by the large carnivores (Section 10.4.1).

I therefore consider my estimate that 21 - 30 % of the large herbivore live mass was removed annually from the Etosha plains to be realistic. Taking the minimum estimate of 21 % removal, it is clear that neither wildebeest nor zebra which together comprise 80 % of the lion's recorded diet (Table 11.1) and 77 % of the recorded cases of anthrax (Table 10.1) can withstand these mortality pressures. Consequently, it is not surprising that wildebeest and zebra, with recruitment rates to the breeding stock of 11 - 18 % and about 8 % respectively (Tables 8.2 and 12.3) are decreasing in numbers at Etosha. The wildebeest population decreased by 24 % and the zebra population by 43 % during the period of study (1974 - 78). These declines were inversely proportional to the different recruitment rates of wildebeest and zebra. For example, the mean recruitment rate of wildebeest was 14,5 % which was 1,8 times higher than that of 8 % for zebra and the decline in zebra numbers was 1,8 times greater than wildebeest.

If the wildebeest and zebra populations decline further, which seems likely at this stage because of the endemic nature of anthrax, then they could become relatively unavailable to hunting lion which would be forced to turn to alternative prey species (Smuts, 1978b). This may in turn result in increased predation on bush and woodland dwellers such as giraffe, kudu and gemsbok.

Finally, the status of springbok at Etosha supports my findings that the combined effect of predation and disease is the major cause of declining wildebeest and zebra numbers. Springbok have increased more than threefold in numbers (9 800 to 32 000) between 1974 - 78. They also died of anthrax (15 % of all anthrax-infested carcases found were springbok; Table 10.1) but apparently not to the extent that wildebeest and zebra died. Also, the relative predation rate of springbok was far lower than either wildebeest or zebra. Springbok constituted 17,8 % of the live mass removal by predators, compared to 65,4 % by wildebeest and zebra combined (Tables 11.1 and 11.2). It can be argued that recording of anthrax and predation in springbok were biased in favour of the larger herbivores because of the rapidity with which springbok carcases are obliterated. This may partly be the case, but it is nullified to a large extent by the fact that Etosha's springbok population increased by a factor of 3,3 in five years. It appears that the differential disease and predation pressures which exist between the springbok population and the wildebeest and zebra populations are justifiable reasons for their respective increase and decreases in numbers.

11.4 CONCLUSIONS

Before the introduction of artificial drinking places at Etosha from 1951 onwards, the cyclical nature of herbivore movements to and from preferred grazing areas was evident (Bigalke, 1961). Refer also in this regard to Section 2.6 in which I review the development of Etosha for tourism. Consequently, in pristine times, the short rainy season provided an abundance of temporary drinking places for grazers such as wildebeest as well as attracting them to the apparently preferred annual grasses in the Okaukuejo area, which are high in nutrients (Section 7.3). However, before the advent of permanent drinking troughs, the migratory herds vacated these "wet season dispersal areas" (Bigalke, 1961) when the ephemeral rainwater pools dried. Thereby a natural, rotational grazing system operated which precluded predators and scavengers from establishing permanent populations in large parts of the Okaukuejo area. Also, in the absence of roads and accompanying gravel pits, the disease factor was not yet epidemic in any part of Etosha (Section 10.4.1).

The provision of artificial watering points in the form of drinking troughs and gravel pits modified the earlier migratory tendencies of herbivores and, at the same time, stabilised the environment for predators and scavengers.

Following on this, the reduced need to migrate has resulted in smaller group sizes of wildebeest (Section 12.4). This in turn makes them more vulnerable to predation and especially increases neo-natal mortality by rendering calves more easily available to hyaena (Smuts, 1978b). In the present study at Etosha, hyaena scats were found to contain foetal and newborn wildebeest calf hooves as well as amounts of wildebeest calf tailhairs (Report No. 1768/77, S.A. Police Forensic Laboratories, 1977). Thus wildebeest and other large herbivores at Etosha have to contend not only with an increased lion population which has expanded spatially, but also with a substantial hyaena population which can alternate efficiently between scavenging and predating. Cheetah may also exert predation pressure on wildebeest calves.

In addition, wildebeest form a major prey item of lion and hyaena. If the combined effects of this predation are coupled to my findings that 62 % of all deaths in wildebeest were caused by disease, namely anthrax (Section 10.3.1), then it follows that the pressure exerted by predators and disease is the major reason for the decline of wildebeest at Etosha during the period of study. Moreover, this assertion is supported by the fact that the quantity and quality of nutrients and water were not limiting during my investigation (Sections 5, 6, 7 and 8). This was also evident in the good nutritional status of the wildebeest (Section 9).

Whereas predation may have a negligible effect in a system such as Serengeti (Schaller, 1972), where herbivore mortality was attributable mostly to malnutrition and disease (Watson, 1967; Bell, 1969; Sinclair, 1977), predation can, under certain circumstances, such as were encountered in Ngorongoro Crater and Kruger Park, have a considerable effect on the herbivore population (Kruuk, 1972; Smuts, 1975, 1976, 1978b, c). It appears that the special conditions at Etosha, which have resulted from man's impact on the environment in the form of fences, roads and artificial drinking places, have created abnormal disease and predation levels, causing wildebeest numbers to decline drastically.

11.5 SUMMARY

11.5.1

The role of predators and scavengers on the Etosha plains was examined in relation to the declining wildebeest population during the period 1974 - 78.

11.5.2

The estimated 285 - 400 lion, which included resident prides and ranging nomads, had a group size of 7,2 and an adult ratio of 1 male : 1,03 females. Immatures comprised 37 % of the sightings. A total of 21 known pride areas or nomadic ranges were located on the plains during the dry season, but the situation in the wet season was unknown. Density was 1 lion/4,5 - 6,3 km^2, which was comparable to other areas in Africa.

11.5.3

Between 50 - 100 cheetah inhabited the plains, with a density of 1 cheetah/18 - 36 km^2. Spotted hyaena numbers were estimated from data of other areas, assuming a ratio of 1 hyaena : 1 lion. This gave an estimated population of 285 - 400 hyaena. Packs of up to 23 hyaena at Etosha indicated frequent hunting and records of kills on zebra, wildebeest, kudu and springbok were obtained. An initial estimate of black-backed jackal numbers (1 000 - 2 000) gave a density of 1 jackal/0,9 - 1,8 km^2, the large population being indicative of a substantial predator population. Up to 52 jackal were seen at one zebra carcass.

11.5.4

Preferred prey species of lion at Etosha were gemsbok, wildebeest, zebra, ostrich and springbok in declining order of magnitude. Cheetah preferred springbok above all else but sometimes killed wildebeest calves. Hyaena showed a preference for wildebeest, followed by zebra and springbok.

11.5.5

Based on a mean daily food intake of 5 % of body mass, the lion, cheetah and hyaena populations on the plains were estimated to require 1 - 1,5 million kilogram of food annually, including uneaten residues. This demand represented a yearly removal of 21 - 30 % from the total live mass of the six major herbivore species, namely wildebeest, zebra, springbok, gemsbok, hartebeest and ostrich.

11.5.6

At Etosha, lion : prey ratios were 1 : 107 - 153 and the ratios of lion/cheetah/hyaena : prey were 72 - 105. These ratios were higher than in most other areas and of the same order as those in the Kruger Park where the predator density was considered high enough to warrant control. Lion biomass at Etosha was also estimated to be higher than at Kruger Park, namely 18,8 - 26,8 kg/km^2 compared to 13,6 - 20,5 kg/km^2.

11.5.7

Predators and scavengers at Etosha benefitted from the surplus of meat which was provided by anthrax-infected carcases. Thereby their numbers may have increased and the combined effects of disease and predation were considered to be the main reason for the decline in wildebeest numbers and also in zebra numbers. Together, wildebeest and zebra formed 80 % of the lion's recorded diet and 77 % of the recorded cases of anthrax. In contrast the springbok population, being relatively much less affected by both disease and predation, increased by a factor of 3,3 during the five-year period.

11.5.8

The overall conclusion reached in this investigation was that the earlier, natural movements of the migratory herbivores at Etosha have been modified by fences, road-building and artificial, permanent drinking places. Disease, especially anthrax, has become endemic in areas where gravel pits occur, while the predator-scavenger populations have stabilised and increased where artificial water has been provided. Furthermore, disease is complementary to predation by providing an abundance of carcases during anthrax epidemics. Taking into account the findings that neither food nor water were limiting to the wildebeest population and the fact that their nutritional status was good, it was evident that disease and predation had combined under the special conditions existing at Etosha and together were the major cause of the decline in wildebeest and also in zebra numbers.

Section 12

POPULATION STRUCTURE

12.1 INTRODUCTION

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

12.1.1 Decline in Total Population

Prior to aerial counts which commenced in 1966, only general estimates of the wildebeest population 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 at Etosha and were subsequently adopted in preference to the previous method of random counting. Thereby 4 773 (1969) and 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 whose numbers dropped from 3 300 to 2 493 (Berry, 1978). The decreasing trend is shown in Fig. 12.1.

12.1.2 Spatial and Temporal Distribution

The seasonal distribution of the wildebeest population is illustrated in Fig. 12.2 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

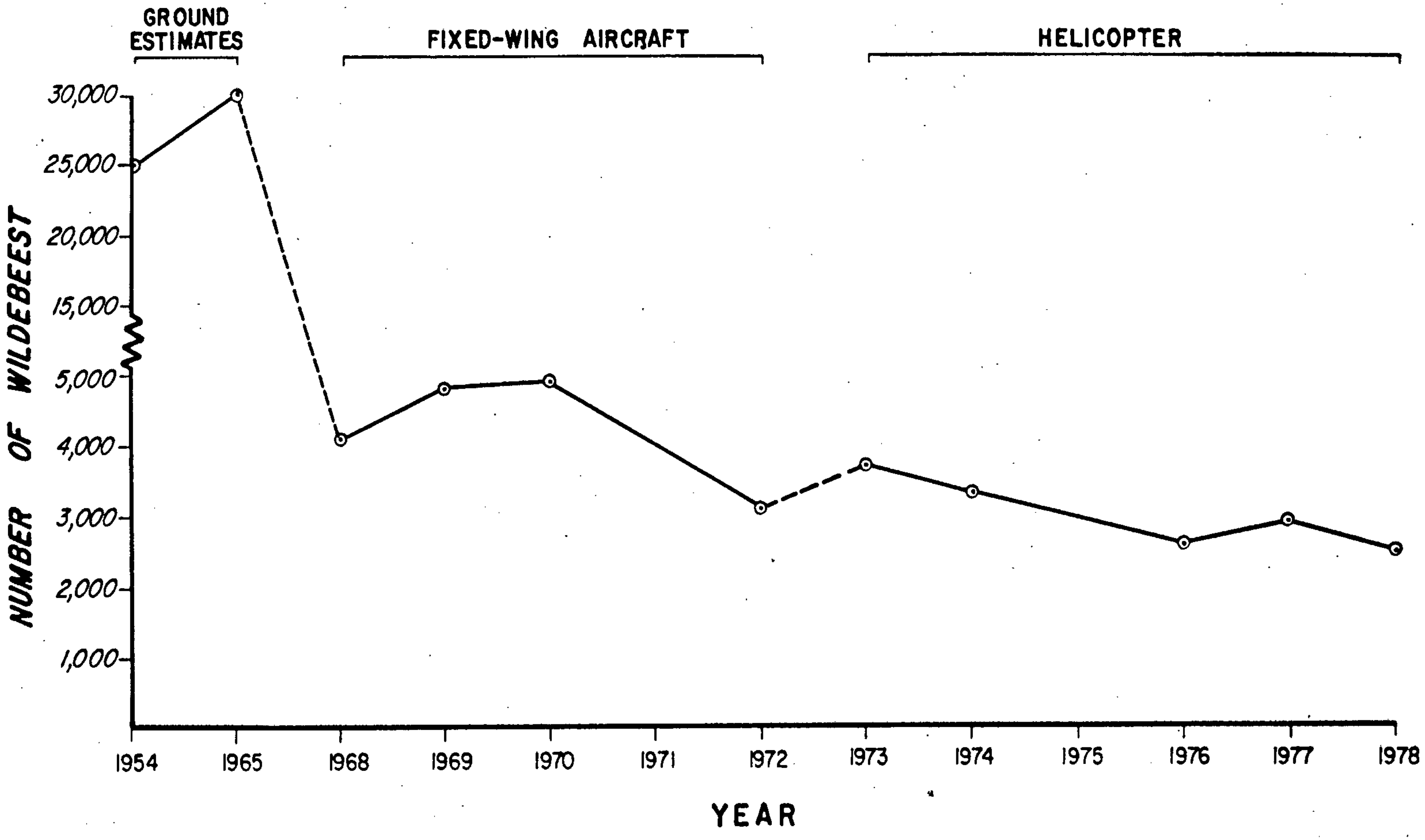

Fig. 12.1 : Estimates and aerial counts of the wildebeest population at Etosha between 1954 and 1978.

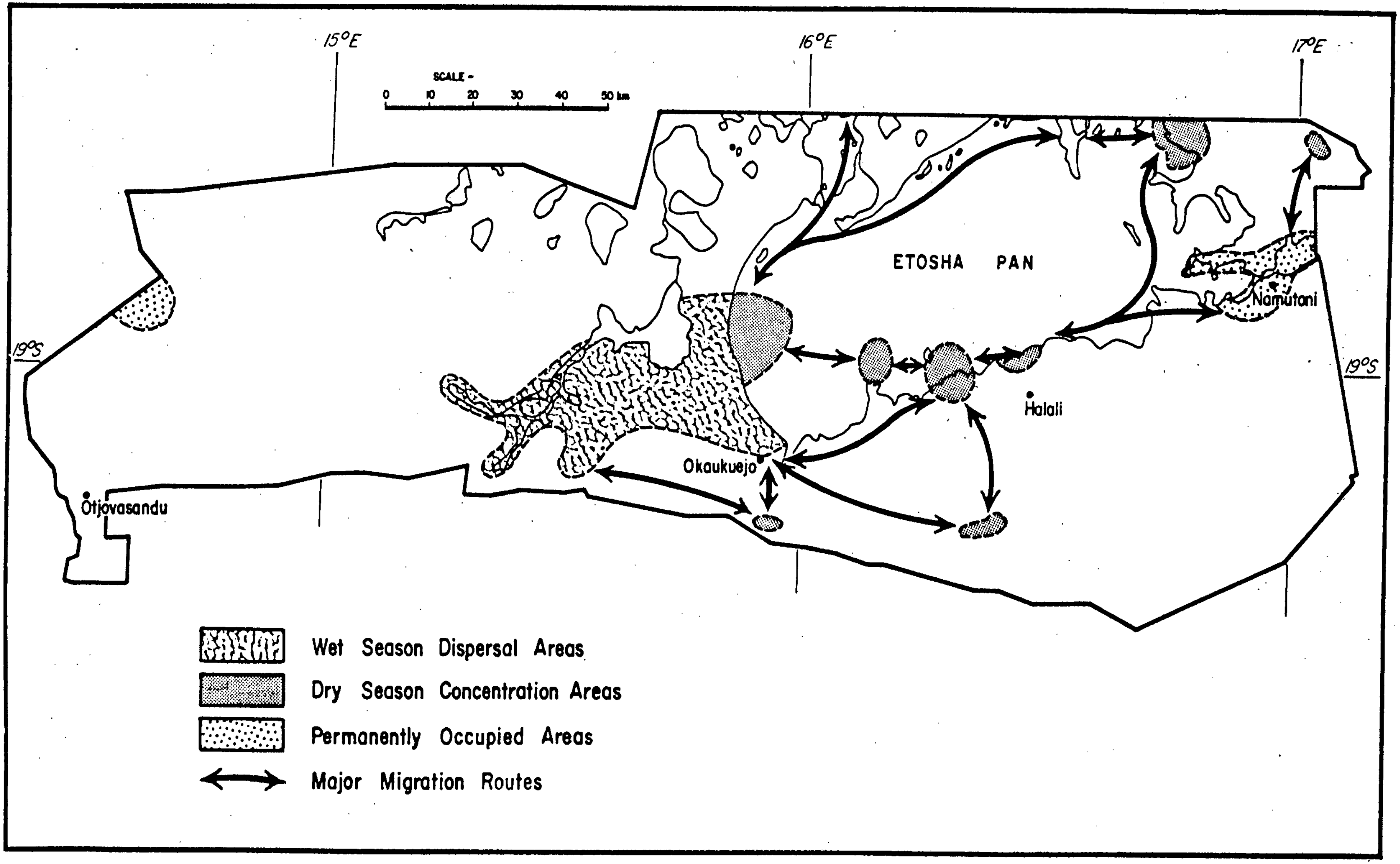

Fig. 12.2 : Seasonal distribution and major migration routes of the wildebeest population at Etosha (1974-78).

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. 12.2). Although some interchange occurred between these groups they occupied discrete areas.

12.2 METHODS

12.2.1 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, 1978 a, b). Since his results were obtained in the thickly vegetated Umfolozi Game Reserve in Zululand, I considered the open grasslands and comparatively sparsely vegetated thorn savanna which wildebeest inhabit at 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.

12.2.2 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 required 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.

12.2.3 Resightings of Marked Wildebeest

During this investigation a total of 60 wildebeest were immobilised and marked with numbered neckbands. I used the Lincoln Index (Overton, 1971) on marked wildebeest which were subsequently resighted in the herds, to estimate the total population. Thus I was able to compare these estimates with the direct counts made from the aircraft.

12.2.4 Age Determination by Tooth Attrition

To establish mortality patterns in wildebeest, a total of 283 skulls were 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. I also established the ratio of maxillary premolar and molar crown height to root length and noted the degree of root apex occlusion. 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 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 x magnification. However, the manifestation of several errors in this technique, such as possible misinterpretation 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.

12.2.5 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 birthrate. 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.

12.3 RESULTS

12.3.1 Estimation of Total Population

The counts made by helicopter and fixed-wing aircraft are given in Table 12.1 and include resightings of marked wildebeest. A second, indirect estimation of the total wildebeest population was obtained by resightings of marked animals from the ground (Table 12.2). The total population was estimated by applying the "urn model" proposed by Overton (1971) for calculating by Lincoln Index and for setting 95 % confidence limits. I considered this model to be the most suitable for my purpose because :

(i) the population was discrete;

(ii) the number of marked animals was known;

(iii) a known sample of observations was made;

(iv) no bias existed in respect to the observation of marked versus unmarked animals.

Thus $\hat{N} = n\,M/x$

where $\hat{N}$ = estimated number of wildebeest at Etosha
n = number of wildebeest sighted
M = number of wildebeest marked
x = number of marked wildebeest sighted

Table 12.1 : Aerial counts of wildebeest at Etosha (1974 - 78)

Year	Month	Numbers Counted							Type of aircraft[**]
		Older than 1 year	Calves	Mixed herds	Bachelor herds	Lone bulls	Marked wildebeest[*]	Total	
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	5	2 638	H
1976	Dec.	2 078	585	1 757	285	32	(6)?	2 659	Fwa
1977	March	2 576	483	2 160	276	140	12	3 059[***]	H
1977	Sept.	2 613	356	2 365	230	18	(17)?	2 969[***]	Fwa
1978	March	2 069	424	1 539	388	142	28	2 493	H
Mean		2 247	537	1 871	300	74	-	2 783	-
± SD		334	124	346	66	49	-	336	-

[*] Marking commenced in June 1976; only helicopter resightings are valid

[**] 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 12.2 : Indirect estimates of total wildebeest population at Etosha by application of the Lincoln Index to marked individuals

Year	Helicopter (H) or Ground (G) count	Criteria used for wildebeest *						Aerial count
		No. sighted (n)	No. marked (M)	No. of marked individuals sighted (x)	95 % confidence limits		Estimated population ($\hat{N}$)	
					Lower	Upper		
1976	(H)	2 638	6	5	1 019	8 120	3 166	2 638
1977	H	3 059	14	12	1 799	6 295	3 569	3 059
1978	H	2 493	30	28	1 752	3 859	2 671	2 493
1978	G**	130,59	29	2,69	282	6 492	1 408	1 453

* Lincoln Index : $\hat{N} = n\,M/x$ with 95 % confidence limits on $1/E(x) = N/nM$
where E = expected value

** Mean values for 39 separate ground counts, thus :
total n = 5 093
total M = 1 131
total x = 105

The results indicate that, on average, aerial and ground counts underestimated the total population by 11 %. However, because the possibility existed that marked wildebeest could have died during the interval between marking and a count, the number of marked individuals (M in the formula) may have been too high. Consequently I did not make any upward adjustment of the aerial counts. Based on field experience, I considered the best estimate of population numbers to be based on 39 separate ground counts (Table 12.2) which overestimated the theoretical population number, as gauged by Lincoln Index, by 3,2 %.

12.3.2 Age-Sex Ratios

Table 12.3 shows the range and mean yearly ratios of the age-sex and social status of wildebeest at 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.

12.3.3 Age-Sex Ratios in Mortality

A total of 15 age classes from birth to approximately 14 years were distinguishable and 197 of the 283 skulls could

Table 12.3 : Structure of the wildebeest population at 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

be accurately sexed (Table 12.4). 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 12.4.

12.3.4 Wildebeest Population Model

The trend in the population total was simulated by applying realistic values for the model's selected parameters (Table 12.5). 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 12.5). Subsequently, I purposely altered each major parameter by an increase of 10 % and a decrease of 10 % (Fig. 12.3) to predict the population trend until 1982. A similar procedure (Shiell and Starfield, 1977) was used on wildebeest and zebra populations

Table 12.4 : Mortality patterns in wildebeest at Etosha (1976 - 78)

Estimated age in years	No. of skulls collected	Percentage of sample	Cumulative total[x]	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

[x] The cumulative total is biased in favour of adult skulls because of the rapidity with which carcases 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 12.5 : Simulation of Etosha's wildebeest population data, using various parameters (1973 - 82)

Year	Mean rainfall (mm)	Parameters				Results					Actual census figures
		Adult lion population	Kill rate	Calf survival rate	Adult birth rate	Calves	Yearlings	2 Year olds	Adults	Total wildebeest population	
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	-	208	1,25	0,5	0,35	521	262	230	1 488	2 500	-
1980	-	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	-

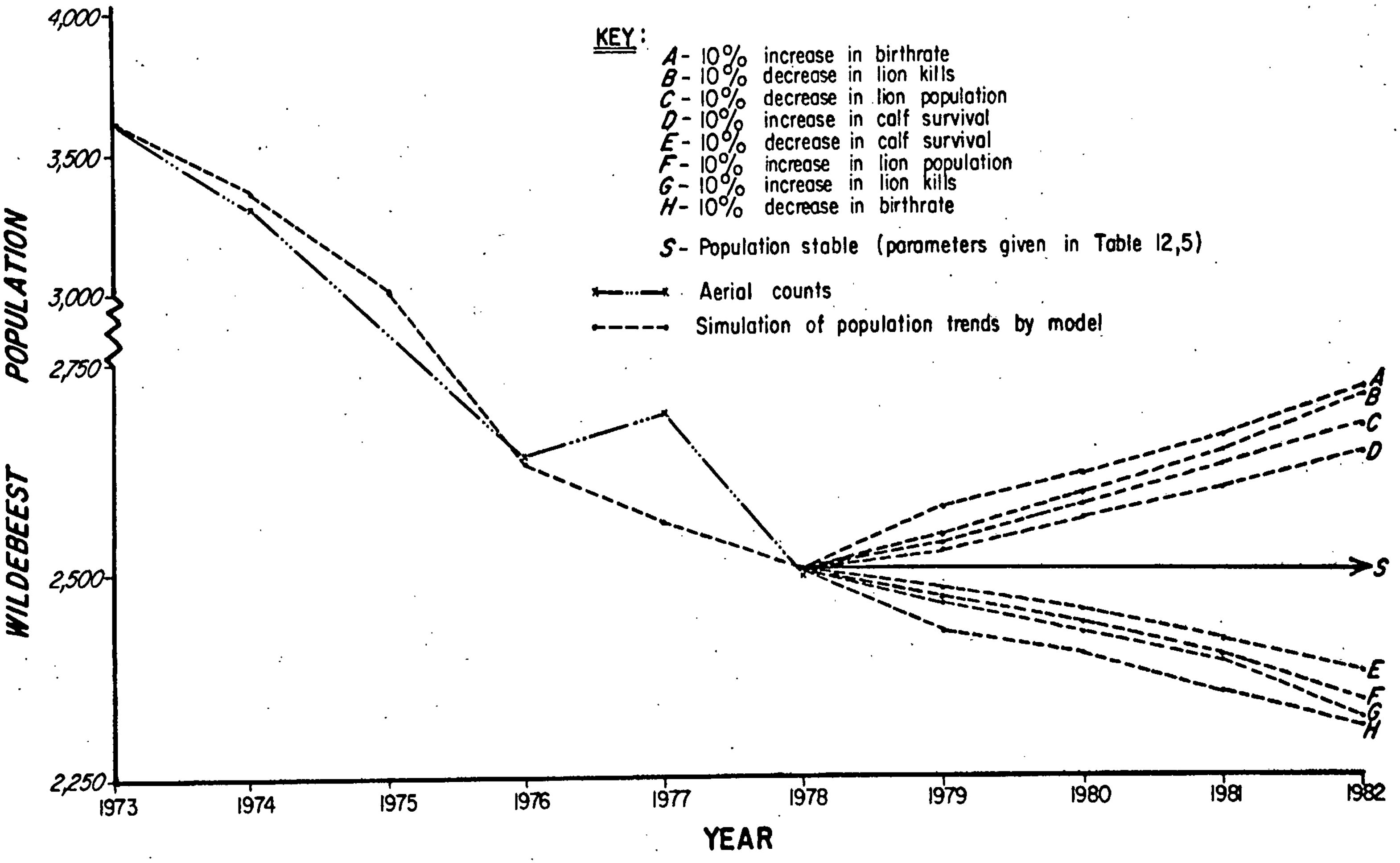

Fig. 12.3 : Wildebeest population model and predictions for future trends at Etosha (1973-82).

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).

12.4 DISCUSSION

12.4.1 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 12.3). 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 12.6 and I have chosen to compare it with the results of a similar investigation by Attwell (1977) which was, however,

Table 12.6 : Population structure of the Etosha wildebeest population (1976 - 78), compared to a Zululand population investigated by Attwell (1977)

Criteria used	Area	
	Etosha[x]	Zululand[xx]
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

[x] Based on ground counts (1976 - 78)

[xx] Based on aerial count (August, 1974)

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 at Etosha and consequently relatively more adult cows in the population (1 bull : 1,57 cows at Etosha, compared to 1 bull : 1,49 cows (Attwell, 1977)). This suggests that bulls at Etosha were subjected to a higher mortality rate and is borne out by the sex ratio from skulls collected at Etosha (Table 12.4) which was 1 bull : 0,38 cows ($X^2 = 146,69$; $P < 0,001$). 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 Kruger 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 at 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 at 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 at 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 at Etosha can be explained by the fact that proportionately fewer and larger breeding herds, each with a herd bull in attendance, existed at Etosha than in Zululand.

Calf survival at Etosha appeared to be higher than in

Zululand (0,5 compared to 0,4; Table 12.7) 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 12.4) 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 at Etosha (89 %). Consequently, 26 % of Zululand's adult wildebeest attained an age of more than 10 years, while at Etosha only 11 % exceeded this age.

Table 12.7 : Comparison of birthrate and calf survival of wildebeest at Etosha with other populations

Area	Mean seasonal rainfall (mm)	Criteria measured (mean)			
		Birthrate		Calf survival	% Calves in total population
		2 year olds	Adults		
Western Masailand East Africa(1)	762	0,83	0,95	0,20	19
Serengeti Nat. Park Tanzania(2)	782	0,37	0,96	0,24	10
Kruger Nat. 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 Nat. Park Rhodesia(5)	550	0,0	0,74	0,49	22
Etosha Nat. 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

In summary, it appeared that the mortality patterns in neonatal calves among Etosha's wildebeest were typically high. Also, up to the age of six years mortality was very similar to declining populations at Kruger Park (Braack, 1973) and Zululand (Attwell, 1977). Adult mortality at 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 Kruger 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 at Etosha (Section 10) appears to have led to an unnatural predator-prey live mass ratio (Section 11). This in turn has resulted in a situation where mortality exceeds the birthrate and a consequent decline in population.

12.4.2 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 birthrate, calf survival which leads to recruitment rate, and mortality of animals older than one year. To simulate conditions at 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 (Section 10). In estimating the adult lion population and their kill rate, I referred to punch card data at Etosha Ecological Institute from 1973 - 1978 and my observations during this study (n = 912 pride compositions; n = 139 wildebeest carcases; Sections 10 and 11).

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 birthrate I calculated that, on average, 63 % of the adult population were cows and that they had a conception rate of 87 % (Table 12.3). Consequently, the upper limit for adult birthrate 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 Kruger National Park where precociousness in two year-olds resulted in a birthrate of 0,21 in this age group (Starfield *et al.*, 1976), I did not record any pregnancy or calving by immature wildebeest at 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, 1976b). 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 birthrate 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 birthrate and calf survival, although birthrate appears to be a very sensitive parameter for change in the population as will be discussed subsequently (Section 12.4.3).

If the Etosha wildebeest population is compared to other free-ranging populations in regard to birthrate and calf survival, then the former parameter is somewhat lower while the latter is considerably higher than most other populations with the exception of Wankie National Park, Rhodesia (Table 12.7). 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 birthrate 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 12.7 a general trend is evident, namely, that well-watered areas which support large populations of wildebeest such as East Africa appear to have higher birthrates than the arid areas of Wankie and Etosha. In Kruger Park and Zululand, both areas of moderate rainfall, wildebeest birthrates 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.

12.4.3 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. 12.3. The order of increasing sensitivity to change is calf survival, lion population, lion kill rate and wildebeest birthrate. The parameters required for an hypothetically stable population are detailed in Table 12.5. 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, 1973b).

The modelled changes of ± 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 birthrate 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 four years into the future (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 birthrate 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 birthrate 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 at 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.

12.5 SUMMARY

12.5.1

Following an apparent drastic decline in the wildebeest population at 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). Marked individuals, released into the free-ranging population, gave an additional method of estimating population size, which, when calculated by Lincoln Index, showed a mean underestimation of 11 % in aerial and ground counts.

12.5.2

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 at 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.

12.5.3

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 corresponded well with those found in two other declining populations except that fewer wildebeest at Etosha survived beyond 10 years and maximum longevity was reduced by about seven years. A combination of disease (anthrax) and predation pressure appeared to be the most likely cause of this early adult mortality.

12.5.4

A computer model was used to simulate the declining population by manipulating the critical parameters of birthrate, calf survival and combined mortality in all other age groups. Plausible mean values were 0,35 for birthrate 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. Birthrate 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 birthrate 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 birthrate appeared to be compensated to a certain extent by a normal to above average calf survival rate.

12.5.5

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.

12.5.6

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.

Section 13

GENERAL SUMMARY AND CONCLUSIONS

> "This variety /̄of antelope̲/ does not exist for our amusement or for our contempt; it has evolved as a complex of creatures making the fullest possible utilization of part of a habitat. . . evolution is, as it were, always probing unoccupied niches or finding new niches."
>
> F. Fraser-Darling (1960)
> *Wild Life in an African Territory*

13.1 INTRODUCTION

In order to understand why the present environment at Etosha has changed to the detriment of the wildebeest population, 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 synthesize the implications of the results obtained in the present study and then make practical recommendations for a management strategy which may help to halt and possibly reverse the decline in wildebeest numbers at Etosha.

13.2 EVOLUTIONARY HISTORY OF AFRICAN UNGULATES

Although the first well-defined Artiodactyla can be traced back to the Eocene, approximately 35^6 - 55^6 yrs BP, the fossil record of Tertiary period mammals indicates that African ungulates appeared 12^6 - 25^6 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 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 at 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.

13.3 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 summary, 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 synthesize 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 synthesize vitamin C. Thus the ruminant is able to contend very satisfactorily with the erratic supply of nutrients produced by a capricious environment.

(ii) The evolvement 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. A possible additional advantage of not being obliged to masticate food thoroughly at the feeding site would be the concealment of the newborn young while the mother moves about foraging for relatively brief periods.

(iii) The specialised limb morphology in artiodactyls by way of a unique, double trochleared 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 intraspecific 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 (Vrbra, 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 neocortex 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 stomach's structure 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 (Keast, 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.

13.4 EXISTING ENVIRONMENTAL CONDITIONS FOR WILDEBEEST AT 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 at Etosha, as evidenced by the present investigation.

13.4.1 Water Requirements

Being a bulk and roughage grazer of grass and therefore dependent on water, wildebeest at 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 at Etosha have therefore enjoyed the advantages of a specialist grazer 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.

13.4.2 Food Requirements

At least 97 % of the diet of wildebeest at 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 synthesize protein in the rumen by microbial action, makes 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.

13.4.3 Reproduction

The high pregnancy rate in adult wildebeest cows at 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 $J.g^{-1}$ compared to 2,91 $J.g^{-1}$ 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.

13.4.4 Climatic Factors

Wildebeest at 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 have not been included in this thesis and they will be reported elsewhere (Berry *et al.*, unpublished data). Nevertheless, for the sake of completeness, it can be stated that Etosha's climate was not considered to be limiting for wildebeest.

13.4.5 Disease and Predation

Apart from anthrax, no other major disease was diagnosed in Etosha's wildebeest. Anthrax featured prominently in all seasons at 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 at Etosha for anthrax, epidemics occur fairly predictably during the rainy season. Etosha's carnivores are apparently not susceptible to anthrax and have, moreover, benefitted from the food supply provided by anthrax-infected carcases. 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 population's demography 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.

13.5 CONCLUSIONS AND RECOMMENDATIONS FOR MANAGEMENT

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 species' ability 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 Park's sanctuary 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 two 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 has been quantitatively demonstrated in this thesis. I wish to reiterate that since the closure of Etosha by fencing, the resident wildebeest population has not been subjected to a drought. As discussed earlier, the food-water link in wildebeest is critical and if drought conditions were to prevail, the population will be subjected to additional environmental pressure.

My recommendations for management to counter the present situation must be based on practical considerations. There are two major options open for consideration : either modify Etosha's boundaries or attempt to manage within the existing boundaries.

13.5.1

Modification of portions of Etosha's present boundaries should be aimed at incorporating some of the original habitat of the migratory wildebeest as well as other migratory species. Essentially this would include two natural features which currently lie in Owambo to the north of Etosha. One is the plains system surrounding Lake Oponono; the other is the Andoni plains system of which the majority lies outside Etosha. Without these two areas, a true migratory situation cannot exist and consequently the previous numbers of plains animals will not be regained. However, any boundary changes to Etosha will affect political geography and would require consensus at the first tier of government. As a result, other factors which are beyond the scope of the present investigation will have to be considered. I nevertheless submit that the expansion of the Etosha conservation area to encompass the Andoni-Oponono region will favour the migratory herds. Moreover, this increased area of conservation could be managed to the benefit of the Owambo people through tourism and possibly wild animal cropping on a sustained yield basis. The present situation is an impasse which may result in further reductions of wildebeest and other large herbivores within Etosha.

13.5.2

Whether the boundaries of Etosha are changed or not, it is essential, not only in the case of wildebeest, but for most other herbivore species as well, to counter the imbalance caused by abnormal levels of disease and predation. Since disease, notably anthrax, appears to be the primary cause of decline in wildebeest numbers within Etosha by direct mortality and secondarily by increases in the predator-scavenger populations, it is imperative that research into the restraint of anthrax at Etosha be extended. Burning of anthrax-infected carcases and closure of gravel pits or their isolation by fencing cannot be considered sufficient, since neither practice can be effectively carried out in an area the size of Etosha. Firstly, it is highly unlikely that all anthrax-infected carcases can be detected and burnt before the disease is spread by agents such as scavengers, insects, water and wind. Secondly, it is also highly unlikely that all animal and bird life which may serve as mechanical carriers of anthrax can be effectively excluded from the hundreds of gravel pits in existence. The anthrax problem is one which will require combined research by veterinarians and ecologists. In addition, it is strongly recommended that the expertise of applied mathematicians be used to assist in building predictive models for anthrax epidemics at Etosha.

13.5.3

The unnatural levels of predators and scavengers at Etosha are a consequence not only of anthrax but also of the artificial drinking places provided for animals. Here there are two possibilities for management. Either the artificial water sources affecting the movements of the plains animals must be closed or the surplus of carnivores must be directly controlled by culling.

I recommend the closure of artificial drinking places in preference to the culling of carnivores for several reasons. These are :

13.5.3.1

Intensive culling of lion and spotted hyaena for a period of four years has met with limited success elsewhere. Lion regained 90 % of their former numbers only 17 months after cessation of culling, while the effects on hyaena were difficult to measure, but indicated a slow recolonisation.

13.5.3.2

It follows from this that the culling of carnivores would have to be a continual process, lasting indefinitely, since we are dealing here with an effect, not a cause. Such an operation will require considerable manpower and equipment.

13.5.3.3

Unpredictable and undesirable side effects may occur when animals such as carnivores, which occupy a tertiary trophic level in the nutrient and energy flow through a system, are injudiciously removed. It will be very difficult, at the present state of our knowledge, to decide correctly just what surplus of carnivores must be culled and also, which age-sex components must be removed. Also, with insufficient data at hand regarding the interrelations between predators, prey and their mutual environment at Etosha, it would be not only premature but unwise to initiate a carnivore culling project.

13.5.3.4

Finally, on aesthetic grounds alone, the intensive, long term culling of predators and scavengers in a proclaimed National Park will not meet with approval of national and international bodies of opinion, including the lay press.

Instead, I firmly recommend that initially, certain artificial water points on the plains of Etosha be closed to alleviate predation pressure. These are Adamax, Leeubron, Gaseb and Gemsbokvlakte in the Okaukuejo area (refer to Fig. 2.1). They must be closed at the height of the rainy season, namely the end of February, to enable water-dependent species in their vicinity to disperse naturally when the rains cease. Closure of these water points during the dry season may result in certain water-dependent species being left stranded in isolation.

The effect of these closures on the large herbivores and carnivores must be monitored and, depending upon the results, decisions should be taken on the closure of other artificial water points.

I also recommend that no further artificial water points be made available to animals at Etosha without supportive research results. The introduction of artificially supplied water into an arid area such as Etosha, must be made with circumspection, taking into account the periodicity of droughts, when primary food production may fail to meet the demands made by the animals.

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APPENDICES

Appendix 1 : List of grasses recorded from the main vegetation zones inhabited by wildebeest at Etosha (1974-78). Species and authors are according to Merxmüller (1972) and the State Herbarium, Windhoek (1980).

Arachne racemosa (Heyne) Ohwi
Andropogon schinzii Hackel
Anthephora pubescens Nees
A. schinzii Hackel
Aristida adscensionis L.
A. congesta Roemer & Schultes
A. effusa Henrard
A. hordeacea Kunth
A. meridionalis Henrard
A. rhiniochloa Hochst
A. scabrivalvis Hackel
A. stipitata Hackel ssp. stipitata
A. stipoides Lam.

Bothriochloa radicans (Lehm) A. Camus
Brachiaria eruciformis (Sibth. & Sm.) Griseb.
B. nigropedata (Munro ex Ficalho & Hiern) Stapf
B. poaeoides Stapf
B. schoenfelderi C.E. Hubb. & Schweik.

Cenchrus ciliaris L.
Chloris virgata Swartz
Craspedorhachis sarmentosa (Hackel) Pilger
Cymbopogon excavatus (Hochst.) Stapf
Cymbosetaria sagittifolia (A. Rich.) Schweik.
Cynodon dactylon (L.) Pers.

Dactyloctenium aegyptium (L.) Beauv.
Danthoniopsis dinteri (Pilger) C.E. Hubbard
Dichanthium papillosum (Hochst. ex A. Rich.) Stapf
Digitaria eriantha Steudel
D. perrottetii (Kunth) Stapf
D. sanguinalis (L.) Scop. ssp. sanguinalis
D. seriata Stapf
D. setivalva Stent
D. smutsii Stent
Dinebra retroflexa (Vahl) Danser
Diplachne fusca (L.) Beauv.
D. cuspidata Launert

Echinochloa colonum (L.) Link
E. holubii (Stapf) Stapf
Eleusine indica (L.) Gaertner
Enneapogon brachystachyus (Jaub. & Spach) Stapf
E. cenchroides (Roemer & Schultes) C.E. Hubbard
E. scaber Lehm
E. scoparius Stapf
Enteropogon macrostachyus (Hochst. ex A.Rich.) Munro ex Benth.
Entoplocamia aristulata (Hackel & Rendle) Stapf
Eragrostis annulata Rendle
E. cilianensis (All.) Vignolo-Lutati
E. cylindriflora Hochst.
E. dinteri Stapf
E. echinochloidea Stapf
E. glandulosipedata De Wint.
E. jeffreysii Hackel
E. laevissima Hackel
E. lehmanniana Nees
E. micrantha Hackel
E. nindensis Fic. & Hiern
E. omahekensis De Wint.
E. pilgerana Dinter ex Pilger
E. pilosa (L.) Beauv.
E. porosa Nees
E. rigidior Pilger
E. rotifer Rendle
E. sabinae Launert
E. superba Peyr.
E. trichophora Coss. & Dur.

Fingerhuthia africana Nees
Heteropogon contortus (L.) Beauv. ex Roemer & Schultes
H. melanocarpus (Elliott) Bentham
Megaloprotachne albescens C.E. Hubbard
Microchloa caffra Nees
Monelytrum luederitzianum Hackel
Odyssea paucinervis (Nees) Stapf
Oropetium capense Stapf
Panicum coloratum L.
P. kalaharense Mez
P. lanipes Mez
P. maximum Jacq.
P. novemnerve Stapf
P. pansum Rendle
P. schinzii Hackel
P. stapfianum Fourc.
Phragmites australis (Cav.) Steudel
Pogonarthria squarrosa (Licht. ex R. & S.) Pilger
P. fleckii (Hackel) Hackel
Pseudobrachiaria deflexa (Schum) Launert
Rhynchelytrum bellespicatum (Rendle) Stapf & C.E. Hubbard
R. brevipilum (Hackel) Chiov.
R. repens (Willd.) C.E. Hubbard
R. villosum (Parl. ex Hooker) Chiov.
Rottboellia exaltata L. f.
Schizachyrium exile (Hochst.) Pilger
Schmidtia kalahariensis Stent
S. pappophoroides Steudel
Sehima ischaemoides Forsk.
Setaria verticillata (L.) Beauv.
S. pallide-fusca (Schum.) Stapf & C.E. Hubbard
Sorghum verticilliflorum (Steud.) Stapf
S. versicolor N.J. Andersson
Sporobolus acinifolius Stapf
S. africanus (Poiret) Robyns & Tournay
S. albicans Nees
S. coromandelianus (Retz) Kunth
S. engleri Pilger
S. ioclades (Trin.) Nees
S. spicatus (Vahl) Kunth
S. tenellus (Sprengel) Kunth (= salsus Mez)
S. virginicus (L.) Kunth
Stipagrostis hirtigluma (Steud. ex Trin & Rupr.) De Wint. ssp. patula (Hack.) De Wint.
S. hochstetterana (Beck. ex Hack.) De Wint.
S. uniplumis (Licht ex R. & S.) De Wint.
Tetrapogon tenellus (Roxb.) Chiov.
Tragus berteronianus Schultes
T. racemosus (L.) All.
Tricholaena monachne (Trin.) Stapf & C.E. Hubbard
Triraphis purpurea Hackel
T. ramosissima Hackel
Urochloa brachyura (Hack.) Stapf

Appendix 2 : List of the larger wild mammal species recorded at Etosha (1974–78).
Dorst and Dandelot's (1970) classification of larger mammals has been used.
Where known, the approximate number of the species is given in brackets.
The mammals kept in the Kaross-Khoabendes quarantine enclosures of Etosha have not been included in this list.

INSECTIVORA	
Erinaceus frontalis	hedgehog
Elephantulus intufti	elephant shrew
Nasilio brachrynchus	" "
LAGOMORPHA	
Lepus capensis	Cape hare
L. saxatilis	southern bush hare
RODENTIA	
Paraxerus cepapi	yellow-footed bush squirrel
Xerus inauris	Cape ground squirrel
X. princeps	Kaokoveld ground squirrel
Pedetes capensis	spring hare
Hystrix africaeaustralis	crested porcupine
PHOLIDOTA	
Manis temmincki	Cape pangolin
PRIMATES	
Galago senegalensis	lesser galago
Papio ursinus	chacma baboon
CARNIVORA	
Canis mesomelas	black-backed jackal (2 000)
Vulpes chama	Cape fox
Otocyon megalotis	bat-eared fox
Lycaon pictus	wild dog (20)
Ictonyx striatus	striped polecat
Mellivora capensis	honey badger
Genetta genetta	common genet
Herpestes pulverulentus nigratus	Cape grey mongoose
H. sanguineus	slender mongoose
Helogale parvula	dwarf mongoose
Mungos mungo	banded mongoose
Cynictis penicillata	red meerkat
Crocuta crocuta	spotted hyaena (500)
Hyaena brunnea	brown hyaena
Proteles cristatus	aardwolf
Felis libyca	African wild cat
F. nigripes	black-footed cat
F. serval	serval
F. caracal	caracal
Panthera leo	lion (500)
P. pardus	leopard
Acinonyx jubatus	cheetah (100)
TUBULIDENTATA	
Orycteropus afer	aardvark
HYRACOIDEA	
Heterohyrax brucei	yellow-spotted dassie
PROBOSCIDEA	
Loxodonta africana	African elephant (2 500)
PERISSODACTYLA	
Equus burchelli	Burchell's zebra (15 000)
E. zebra hartmannae	Hartmann's zebra (800)
Diceros bicornis	black rhinoceros (150)
ARTIODACTYLA	
Phacochoerus aethiopicus	warthog
Giraffa camelopardalis angolensis	southern giraffe (1 000)
Taurotragus oryx	Cape eland (200)
Tragelaphus strepsiceros	greater kudu (3 000)
Oryx gazella	gemsbok (3 000)
Hippotragus equinus	roan antelope (20)
Alcelaphus caama	red hartebeest (200)
Connochaetes taurinus	blue wildebeest (2 500)
Aepyceros melampus petersi	black-faced impala (100)
Antidorcas marsupialis	springbok (32 000)
Sylvicapra grimmia	Grimm's duiker
Oreotragus oreotragus	klipspringer
Raphicerus campestris	steenbok
Rhynchotragus kirki	Damaraland long snouted dik-dik

Appendix 3 : List of wild mammal species referred to in the text, which do not occur at Etosha (1974-78)

Species or sub-species	Common name
Aepyceros melampus melampus	southern impala
A. melampus rendilis	East African impala
Alcelaphus buselaphus cokei	Coke's hartebeest
Alces alces gigas	Alaskan moose
Camelus dromedarius	camel
Cervus canadensis	Rocky mountain elk
C. elaphus	red deer
Connochaetes gnou	black wildebeest
Damaliscus lunatus	tsessebe
Gazella thomsoni	Thomson's gazelle
Hippopotamus amphibius	hippopotamus
Hippotragus niger	sable antelope
Odocoileus hemionus virginianus	white-tailed deer
Ourebia ourebi	oribi
Rangifer tarandus	barren-ground caribou/ reindeer
Redunca arundinum	southern reedbuck
Syncerus caffer	African buffalo

Appendix 4 : Field check list for recording activity of wildebeest during focal - animal studies and the prevailing environmental data at Etosha

Fortran coding sheet column number	Field data required
1	Year (7 or 8)
2 and 3	Month (01 to 12)
4 and 5	Day (01 to 31)
6 and 7	Hour (00 to 24)
8 and 9	Minute (00 to 60)
10	Cloud cover = 0 to 8 oktas
11	Wind speed = 0 to 9 Beaufort scale
12	Wind direction = 0 is calm
	= 1 to 8 clockwise compass points
	= 9 designates a dust storm
13 and 14	Shade temperature = 00 to 50 °C
	= 91 to 99 designates -1 °C to -9 °C
15 and 16	Sun temperature = 00 to 70 °C (black bulb thermometer)
17 and 18	Relative humidity = 01 to 99 %
	= 00 designates dew present
19 and 20	Daily rainfall = 00 to 99 mm as recorded at 08 h 00 at the nearest of four field stations
21 and 22	Map grid reference = 00 to 96 horizontal
23 and 24	= 00 to 32 vertical
25	Vegetation type = 0 to 9
	where : 0 = open pans and bare ground
	1 = short grassland (<50 cm height)
	2 = tall grassland (>50 cm height)
	3 = shrub savanna
	4 = thorn savanna and scrub
	5 = broad - leafed, wooded savanna
	6 = thickets
	7 = river beds and water courses
	8 = mixed vegetation
	9 = transitional zones
26	Vegetation height = 0 to 9
	where : 0 = no vegetation visible
	1 = vegetation up to 15 cm height
	2 = " " " 30 cm "
	3 = " " " 60 cm "
	4 = " " " 1 m "
	5 = " " " 2 m "
	6 = " " " 3 m "
	7 = " " " 4 m "
	8 = " " " 5 m "
	9 = vegetation above 5 m "
27	Horizontal visibility = 1 to 5
	where : 1 = good up to 10 m
	2 = good up to 50 m
	3 = good up to 100 m
	4 = good up to 1 000 m
	5 = good beyond 1 km
28	Age - sex = 0 to 9
	where : 0 = bull - unknown age
	1 = bull - lone, territorial
	2 = bull - adult in bachelor herd
	3 = bull - adult in mixed herd
	4 = bull - immature and sub - adult (1 - 3 yrs)
	5 = bull - calf (<1 yr)
	6 = cow - unknown age
	7 = cow - adult
	8 = cow - immature and sub - adult (1 - 3 yrs)
	9 = cow - calf (<1 yr)

Appendix 4 : (continued)

Fortran coding sheet column number	Field data required
	ACTIVITY = 000 to 900 seconds
29 to 31	where : resting, lying (including ruminating and comfort movements)
32 to 34	resting, standing (including ruminating and comfort movements)
35 to 37	grazing, stationary or slight forward movement
38 to 40	grazing, walking
41 to 43	walking, unrelated to intraspecific social behaviour
44 to 46	trotting, unrelated to intraspecific social behaviour
47 to 49	galloping, unrelated to intraspecific social behaviour
50 to 52	shading, lying
53 to 55	shading, standing
56 to 58	drinking seasonal water (rainwater pools)
59 to 61	drinking perennial water (permanent fountains or drinking troughs)
62 to 64	suckling (by calf or cow)
65 to 67	social encounters (including all overt forms of territorial, fighting, threat, dominance, submissive, displacement and excitement displays)
68	Other specific encounters = 0 to 9 where : 0 = none 1 = copulation 2 = birth 3 = death 4 = death by predation 5 = death by disease 6 = bull killed by predator 7 = cow killed by predator 8 = bull killed by disease 9 = cow killed by disease
69	Influence of other species = 0 to 9 where : 0 = no visible influence 1 = influenced by lion 2 = influenced by hyaena 3 = influenced by jackal 4 = influenced by zebra 5 = influenced by springbok 6 = influenced by gemsbok 7 = influenced by ostrich 8 = influenced by combination of herbivores 9 = influenced by other species
70	Unnatural disturbance during focal time = 0 to 2 where : 0 = none 1 = disturbance due to observer 2 = disturbance due to tourist vehicle or aeroplane
71	Distance moved during focal time = 0 to 9 where : 0 = none 1 = up to 50 m 2 = up to 100 m 3 = up to 200 m 4 = up to 300 m 5 = up to 400 m 6 = up to 500 m 7 = up to 750 m 8 = up to 1 000 m 9 = more than 1 km
72	Distance of focal animal from nearest other wildebeest = 0 to 4 (0 takes preference) where : 0 = among other wildebeest 1 = up to 100 m from other wildebeest 2 = up to 1 km from other wildebeest 3 = more than 1 km from other wildebeest 4 = no other wildebeest in sight
73	Distance of focal animal from nearest other herbivore = 0 to 4 (0 takes preference) where : 0 = among other species 1 = up to 100 m from other species 2 = up to 1 km from other species 3 = more than 1 km from other species 4 = no other species in sight
74 to 76	Net viewable time = 000 to 900 seconds
77 to 79	Total focal sampling time = 900 seconds

Appendix 5: Example of a completed coding sheet, giving data for 24 x 15-minute samples of the activity of a wildebeest at Etosha

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NOTE: A blank space is equivalent to zero

FORTRAN Coding Form

PROGRAM ETOSHA WILDEBEEST FOCAL - ANIMAL STUDY

PROGRAMMER ZOOLOGY DEPARTMENT

DATE 17 JUNE 1977

PUNCHING INSTRUCTIONS

GRAPHIC

PUNCH

PAGE 1 OF FOCAL

CARD ELECTRO NUMBER*

STATEMENT NUMBER

FORTRAN STATEMENT

IDENTIFICATION SEQUENCE

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7 6170815233131346  66183354    69187182131  5  6               320   4 19  9
7 6170845133141444  66183444    21738 95 28                      18 403  9  9
7 6170915143171842  66183444    62609157 60    12                    23 29  9
7 6170945153181939  65183444   179647 62                         12   2 19  9
7 6171015162202036  65183444   274234155 92                     145  25 29  9
7 6171045162212133  65183354330545  6                            19     29  9
7 6171115162212131  65183344842058                                      29  9
7 6171145162222231  65183344   779 10                           111     29  9
7 6171215162232331  65183344   104 35 46532                     183   7 29  9
7 6171245152232430  65183344100 92661                            47   1 19  9
7 6171315152242528  65183344900                                         29  9
7 6171345242252627  65183344900                                         19  9
7 6171415232252626  65183344   479 76 18277                      50   4 19  9
7 6171445132262722  65183344    18870  9        3                     1 19  9
7 6171515132272821  65183344   408 79   413                           5 19  9
7 6171545132242422  65188644900                                         29  9
7 6171615132252522  65188644900                                         19  9
7 6171645122242521  65188644557258                               85   1 29  9
7 6171715112252521  65188644   606 12   170                     112   1 29  9
7 6171745103242422  65183344    65765 70                                29  9
7 6171815003222222  65183334   138217545                                19  9
7 6171845003202024  65183334   215 42586                         57   1 19  9
7 6171915003171725  65183334      431213256                           2 29  9
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Appendix 6 : Field check list for recording activity of wildebeest herds by the instantaneous scan method and prevailing environmental data at Etosha

Fortran coding sheet column number	Field data required
1	First or second coding sheet used for the scan, always entered as "1" or "2" respectively
2 to 10 (reserved for 1st or 2nd coding sheets)	Year (7 or 8) Month (01 to 12) Day (01 to 31) Hour (00 to 24) Minute (00 to 60)
11 and 12	Sun temperature = 00 to 70 °C (black bulb thermometer) = 91 to 99 designates −1 °C to −9 °C
13	Wind speed = 0 to 9 Beaufort scale
14 and 15	Daily rainfall = 00 to 99 mm as recorded at 08 h 00 at the nearest of four field stations
16 and 17	Map grid reference = 00 to 96 horizontal
18 and 19	= 00 to 32 vertical
20	Vegetation type = 0 to 9 where : 0 = open pans and bare ground 1 = short grasslands (<50 cm height) 2 = tall grassland (>50 cm height) 3 = shrub savanna 4 = thorn savanna and scrub 5 = broad – leafed, wooded savanna 6 = thickets 7 = river beds and water courses 8 = mixed vegetation 9 = transitional zones
21	Vegetation height = 0 to 9 where : 0 = no vegetation visible 1 = vegetation up to 15 cm height 2 = " " " 30 cm " 3 = " " " 60 cm " 4 = " " " 1 m " 5 = " " " 2 m " 6 = " " " 3 m " 7 = " " " 4 m " 8 = " " " 5 m " 9 = vegetation above 5 m "
22 to 77 (1st coding sheet) 11 to 66 (2nd coding sheet) viz:	SEX – AGE – ACTIVITY categories, giving number of wildebeest (02 to 99) in a scan group engaged in a defined activity

	Sex – age	Activity
22 and 23	Unknown	resting (including lying, standing, ruminating and comfort movements)
24 and 25	"	grazing (including stationary and forward movement)
26 and 27	"	purposeful movement unrelated to intraspecific social behaviour (including walking, trotting, galloping, predator evasion and migration)
28 and 29	"	shading, lying or standing
30 and 31	"	drinking seasonal water (rainwater pools)
32 and 33	"	drinking perennial water (permanent fountains or troughs)
34 and 35	"	social encounters (including all overt forms of territorial, fighting, threat, dominance, submissive, displacement and excitement displays)
36 and 37	Full-grown animal of unknown sex	resting
38 and 39	"	grazing
40 and 41	"	purposeful movement
42 and 43	"	shading
44 and 45	"	drinking seasonal water
46 and 47	"	drinking perennial water
48 and 49	"	social encounters
50 and 51	Bull, adult in bachelor herd	resting
52 and 53	"	grazing
54 and 55	"	purposeful movement
56 and 57	"	shading
58 and 59	"	drinking seasonal water
60 and 61	"	drinking perennial water
62 and 63	"	social encounters

Appendix 5: Example of a completed coding sheet, giving data for 24 x 15-minute samples of the activity of a wildebeest at Etosha

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NOTE: A blank space is equivalent to zero

FORTRAN Coding Form

PROGRAM ETOSHA WILDEBEEST FOCAL – ANIMAL STUDY
PROGRAMMER ZOOLOGY DEPARTMENT
DATE 17 JUNE 1977
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PUNCH
PAGE 1 OF FOCAL
CARD ELECTRO NUMBER*

STATEMENT NUMBER | FORTRAN STATEMENT | IDENTIFICATION SEQUENCE

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7 6170745223111147  66183354    65815 20                              2 29  9
7 6170815233131346  66183354    69187182131  5  6               320   4 19  9
7 6170845133141444  66183444    21738 95 28                      18 403  9  9
7 6170915143171842  66183444    62609157 60    12                    23 29  9
7 6170945153181939  65183444   179647 62                         12   2 19  9
7 6171015162202036  65183444   274234155 92                     145  25 29  9
7 6171045162212133  65183354330545  6                            19     29  9
7 6171115162212131  65183344842058                                      29  9
7 6171145162222231  65183344   779 10                           111     29  9
7 6171215162232331  65183344   104 35 46532                     183   7 29  9
7 6171245152232430  65183344100 92661                            47   1 19  9
7 6171315152242528  65183344900                                         29  9
7 6171345242252627  65183344900                                         19  9
7 6171415232252626  65183344   479 76 18277                      50   4 19  9
7 6171445132262722  65183344    18870  9        3                     1 19  9
7 6171515132272821  65183344   408 79   413                           5 19  9
7 6171545132242422  65188644900                                         29  9
7 6171615132252522  65188644900                                         19  9
7 6171645122242521  65188644557258                               85   1 29  9
7 6171715112252521  65188644   606 12   170                     112   1 29  9
7 6171745103242422  65183344    65765 70                                29  9
7 6171815003222222  65183334   138217545                                19  9
7 6171845003202024  65183334   215 42586                         57   1 19  9
7 6171915003171725  65183334      431213256                           2 29  9
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Appendix 6 : (continued)

Fortran coding sheet column number	Field data required	
64 and 65	Bull, immature in bachelor herd	resting
66 and 67	"	grazing
68 and 69	"	purposeful movement
70 and 71	"	shading
72 and 73	"	drinking seasonal water
74 and 75	"	drinking perennial water
76 and 77 (end of 1st coding sheet)	"	social encounters
(start of 2nd coding sheet)		
11 and 12	Bull, adult in mixed herd	resting
13 and 14	"	grazing
15 and 16	"	purposeful movement
17 and 18	"	shading
19 and 20	"	drinking seasonal water
21 and 22	"	drinking perennial water
23 and 24	"	social encounters
25 and 26	Cow, adult in mixed herd	resting
27 and 28	"	grazing
29 and 30	"	purposeful movement
31 and 32	"	shading
33 and 34	"	drinking seasonal water
35 and 36	"	drinking perennial water
37 and 38	"	social encounters
39 and 40	Immature, in mixed herd	resting
41 and 42	"	grazing
43 and 44	"	purposeful movement
45 and 46	"	shading
47 and 48	"	drinking seasonal water
49 and 50	"	drinking perennial water
51 and 52	"	social encounters
53 and 54	Calf, in mixed herd	resting
55 and 56	"	grazing
57 and 58	"	purposeful movement
59 and 60	"	shading
61 and 62	"	suckling
63 and 64	"	drinking water
65 and 66	"	social encounters
67	Unnatural disturbance during scan = 0 to 2 where : 0 = none 1 = disturbance due to observer 2 = disturbance due to tourist vehicle or aeroplane	
68	Distance moved since previous scan = 0 to 9 where : 0 = none 1 = up to 50 m 2 = up to 100 m 3 = up to 200 m 4 = up to 300 m 5 = up to 400 m 6 = up to 500 m 7 = up to 750 m 8 = up to 1 000 m 9 = more than 1 km	
69 and 70	Number of wildebeest in scan group = 02 to 99	
71 to 73 (end of 2nd coding sheet)	Time taken to scan group = 001 to XXX seconds	

Appendix 7 : Focal animal study of wildebeest activity patterns at Etosha (1977 - 78), giving the percentage of time, on a monthly basis, spent by six various age and sex classes of wildebeest, in 13 different activity categories

Month	Age and sex class	Percentage activity												
		Resting, lying	Resting, standing	Grazing, stationary	Grazing, moving	Walk	Trot	Gallop	Shading, lying	Shading, standing	Drinking seasonal water	Drinking perennial water	Suckling	Social encounters
January 1978	Lone, territorial bull	20,4	16,9	45,8	4,4	11,7	-	0,2	-	-	-	-	-	0,6
	Adult cow with calf	7,2	20,4	39,7	0,5	7,8	0,1	1,1	5,0	17,3	0,3	-	0,6	-
	Yearling bull,mixed herd	12,7	8,4	57,1	6,8	14,1	-	0,3	-	-	0,3	-	-	0,3
	Yearling cow, mixed herd	22,0	7,8	47,8	5,3	16,2	0,1	0,5	-	-	0,3	-	-	0,1
February 1978	Adult bull in bachelor and mixed herd	24,6	15,4	39,7	3,9	13,2	-	1,8	-	-	-	-	-	1,4
	Adult cow with calf	36,7	8,9	48,6	1,8	2,0	0,1	1,2	-	-	0,1	-	0,6	-
	Newborn bull calf	65,5	24,4	-	-	5,9	0,2	1,4	0,7	-	-	-	1,1	1,8
	Newborn cow calf	66,4	22,9	-	-	7,2	0,1	1,2	0,4	-	-	-	0,5	1,3
March 1978	Adult bull in mixed herd	27,0	23,8	24,1	1,0	18,8	-	0,6	-	0,2	0,2	-	-	4,3
	Adult cow with calf	7,9	19,1	21,1	2,6	7,3	-	0,3	7,6	33,7	-	-	0,3	0,1
	1 month old bull calf	64,0	12,8	17,6	-	3,8	0,1	0,3	0,4	0,4	-	-	0,2	0,4
	1 month old cow calf	57,9	18,0	17,3	0,4	4,2	-	0,1	0,8	0,3	-	-	0,5	0,5
April 1978	Adult bull in mixed herd	16,2	27,6	22,9	2,3	17,2	-	4,2	-	-	-	-	-	9,6
	Adult cow with yearling calf	2,3	15,0	30,5	4,5	8,3	-	0,2	14,1	23,3	0,2	-	0,1	1,5
	2 month old bull calf	29,0	18,7	22,8	2,3	19,6	0,1	1,5	0,6	4,1	0,5	-	0,4	0,4
	2 month old cow calf	35,2	9,2	24,4	1,0	3,1	-	0,1	17,9	8,2	-	-	0,1	0,2
May 1978	Adult bull in mixed herd	23,5	26,1	27,0	1,8	15,9	0,1	1,7	-	-	-	0,8	-	3,1
	Adult cow with - without calf	28,3	29,4	31,8	1,5	7,6	-	-	-	-	-	0,6	-	1,9
	3 month old bull calf	24,4	7,2	36,6	4,9	16,8	-	0,5	5,2	3,8	-	0,5	-	0,1
	3 month old cow calf	17,6	15,1	30,4	1,8	24,1	0,1	1,0	8,3	0,7	-	0,2	0,2	0,5
May 1977	Lone, territorial bull	10,9	19,6	22,5	10,2	32,8	-	1,3	-	-	-	0,5	-	2,2
	Adult cow without calf	18,8	12,0	34,9	11,2	21,6	0,1	1,0	-	-	-	0,3	-	0,1

Appendix 7 : (continued)

Month	Age and sex class	Percentage activity												
		Resting, lying	Resting, standing	Grazing, stationary	Grazing, moving	Walk	Trot	Gallop	Shading, lying	Shading, standing	Drinking seasonal water	Drinking perennial water	Suckling	Social encounters
June 1977	Lone, territorial bull	39,9	41,0	13,3	1,2	1,9	-	0,1	-	-	-	-	-	2,6
	Adult cow with calf	21,2	23,8	24,5	11,1	17,3	0,1	0,9	-	-	-	0,8	-	0,3
	1,5 year old bull in mixed herd	30,2	22,3	27,7	4,1	9,5	-	0,1	-	-	-	-	-	6,1
	1,5 year old cow in mixed herd	55,0	7,4	24,4	8,8	4,3	-	0,1	-	-	-	-	-	-
July 1977	Lone, territorial bull	22,6	38,9	16,8	1,7	19,3	0,1	0,1	-	-	-	0,5	-	-
	Adult cow with calf	19,3	32,0	27,3	1,7	17,6	0,1	1,2	-	-	-	0,5	0,2	0,1
	1,5 year old bull in mixed herd	27,9	29,5	25,4	5,3	10,9	0,1	0,3	-	-	-	0,3	-	0,3
	1,5 year old cow in mixed herd	49,7	17,2	16,3	2,4	13,7	-	0,3	-	-	-	-	-	0,4
August 1977	Adult bull in mixed herd	22,3	13,8	28,8	9,3	24,2	0,2	0,6	-	-	-	0,6	-	0,2
	Adult cow with calf	43,8	24,8	26,3	3,1	1,9	-	-	-	-	-	-	-	0,1
	1,5 year old bull in mixed herd	37,1	21,3	20,7	10,3	10,5	-	-	-	-	-	-	-	0,1
	6 month old cow in mixed herd	61,7	19,8	12,1	2,9	1,7	-	0,1	1,3	-	-	-	-	0,4
September 1977	Adult bull in mixed herd (nocturnal study)	39,2	11,1	34,6	3,2	10,1	-	0,6	-	-	-	-	-	1,2
	Adult cow with calf	21,0	27,3	35,8	8,1	6,3	-	0,5	-	-	-	0,9	-	0,1
	1,5 year old bull in mixed herd	27,6	15,8	41,8	3,9	9,3	-	0,7	-	-	-	0,6	-	0,3
	1,5 year old cow in mixed herd	47,8	19,3	14,5	4,9	12,5	-	0,2	-	-	-	-	-	0,8
October 1977	Lone, territorial bull	22,7	30,7	10,3	5,1	30,1	-	0,2	-	-	-	0,9	-	-
	Adult cow with calf	37,9	12,9	24,5	5,4	17,5	0,1	1,0	-	-	-	0,5	-	0,2
	1,5 year old bull in mixed herd	29,2	12,3	33,6	5,9	18,4	-	-	-	-	-	0,3	-	0,3
	8 month old cow in mixed herd	39,9	16,1	19,1	1,8	22,5	-	0,1	-	-	-	0,4	0,1	-
December 1977	Adult bull in bachelor herd	29,7	18,0	35,0	1,1	15,2	0,1	0,3	-	-	-	0,4	-	0,2
	Adult cow without calf	27,2	17,3	35,6	4,1	15,0	-	0,7	-	-	0,1	-	-	-
	2 year old bull in mixed herd	2,5	3,6	60,2	7,1	25,4	-	0,2	0,9	-	-	-	-	0,1
	2 year old cow in mixed herd	6,3	25,1	41,4	6,0	20,8	-	0,1	-	-	0,1	-	-	0,2

Appendix 8 : Chi - square analysis of differences in activity of wildebeest at Etosha, during one year, using the focal animal method

Age and sex classes compared	Activity compared	Total seconds recorded (corrected)		Calculated X^2 values ($P<0,001$ at 10,827)	Conclusion
Adult bull versus adult cow	resting	bull = 97 533	cow = 102 833	70,10	bulls rest less than cows
	grazing	= 60 345	= 71 370	461,42	bulls graze less than cows
	movement	= 35 397	= 22 274	1 493,07	bulls move more than cows
	social encounters	= 4 095	= 788	1 119,83	bulls are socially more active than cows
Immature bull v. immature cow (1 - 2 years old)	resting	bull = 35 407	cow = 49 536	1 175,07	bulls rest less than cows
	grazing	= 39 950	= 28 712	919,67	bulls graze more than cows
	movement	= 12 762	= 12 337	3,60	bulls and cows move equally
	social encounters	= 1 278	= 270	328,19	bulls are socially more active than cows
Adult bull v. immature bull	resting	adult = 66 086	imm. = 53 389	675,68	adults rest more than immatures
	grazing	= 40 494	= 51 567	665,92	adults graze less than immatures
	movement	= 20 690	= 17 964	77,48	adults move more than immatures
	social encounters	= 396	= 252	16,00	adults are socially more active than immatures
Adult cow v. immature cow	resting	adult = 43 022	imm. = 49 536	229,22	adults rest less than immatures
	grazing	= 33 911	= 28 682	218,41	adults graze more than immatures
	movement	= 12 365	= 12 337	0,02	adults and immatures move equally
	social encounters	= 90	270	45,00	adults are socially less active than immatures + (+ see text for explanation)
Adults v. calves (<1 year old)	resting	adult = 107 358	calf = 122 963	528,64	adults rest less than calves
	grazing	= 69 526	= 35 172	5 636,20	adults graze more than calves
	movement	= 34 570	= 20 956	1 668,96	adults move more than calves
	social encounters	= 3 929	= 860	983,37	adults are socially more active than calves
Immatures v. calves	resting	imm. = 23 670	calf = 26 324	70,45	immatures rest less than calves
	grazing	= 12 690	= 6 462	6 002,47	immatures graze more than calves
	movement	= 5 202	= 4 392	34,19	immatures move more than calves
	social encounters	= 72	72	0	immatures and calves are socially equally active
Newborn bull calf v. newborn cow calf (<1 week old)	resting	bull = 16 195	cow = 16 082	0,20	both sexes rest equally
	grazing	= 0	= 0	0	neither sex grazes
	movement	= 1 351	= 1 530	5,56	both sexes move equally
	social encounters	= 398	= 585	10,71	both sexes are socially equally active

Appendix 9 : Detailed population energy budget for wildebeest at Etosha during one year (1977/78)

Age - sex and social class	Percentage of population	Number in population	Energy category	Energy required per individual		Population energy budget	
				(kcal.year $^{-1}$)	(kJ.year $^{-1}$)	(kcal.year $^{-1}$)	(kJ.year $^{-1}$)
Calves	20	498	maintenance and activity	704 465	2 947 480	350 823 570	1 467 845 817
			growth	517 961	2 167 149	257 944 578	1 079 240 114
			homeothermy	19 908	83 295	9 914 184	41 480 946
Immature and sub - adult cows (1 - 3 years)	13	325	maintenance and activity	1 464 533	6 127 607	475 973 225	1 991 471 973
			growth	581 478	2 432 904	188 980 350	790 693 784
			homeothermy	38 202	159 837	12 415 650	51 947 080
Immature and sub - adult bulls (1 - 3 years)	10	248	maintenance and activity	1 677 927	7 020 446	416 125 896	1 741 070 749
			growth	749 294	3 135 046	185 824 912	777 491 432
			homeothermy	41 932	175 443	10 399 136	43 509 985
Adult, non - reproductive cows	3	75	maintenance and activity	1 884 269	7 883 780	141 320 175	591 283 612
			homeothermy	49 569	207 397	3 717 675	15 554 752
Adult, reproductive cows	30	748	maintenance and activity	1 884 269	7 883 780	1 409 433 212	5 897 068 559
			gestation	63 769	266 810	47 699 212	199 573 503
			lactation	462 120	1 933 510	251 525 744	1 052 383 713
			homeothermy	49 569	207 397	37 077 612	155 132 729
Adult bulls	24	599	maintenance and activity	2 113 328	8 842 165	1 265 883 472	5 296 456 447
			homeothermy	53 875	225 413	32 271 125	135 022 387
Totals	100	2 493		12 356 468	51 699 462	5 097 329 728	21 327 227 582

Appendix 10: Estimation of daily nitrogen requirement in individual wildebeest at Etosha, on a seasonal basis. Explanation of the detailed requirements is given in the text.

Age—sex and social class	Seasonal nitrogen requirements ($g.day^{-1}$)																				
	Wet, hot (Jan. to Apr.)							Dry, cold (May to Aug.)							Dry, hot (Sept. to Dec.)						
	Maintenance		Growth		Gestation (Q_{np})	Lactation (Q_{nl})	Daily total	Maintenance		Growth		Gestation (Q_{np})	Lactation (Q_{nl})	Daily total	Maintenance		Growth		Gestation (Q_{np})	Lactation (Q_{nl})	Daily total
	EUN	MFN	Q_{ng}	Q_{nh}				EUN	MFN	Q_{ng}	Q_{nh}				EUN	MFN	Q_{ng}	Q_{nh}			
Calf (0–1yr)	1,93	0,46	8,05	0,17	-	-	10,61	3,06	0,73	8,05	0,26	-	-	12,10	4,09	1,32	8,05	0,35	-	-	13,81
Immature cow (1–2yrs)	4,98	2,81	5,02	0,43	-	-	13,24	5,58	2,18	5,02	0,48	-	-	13,26	6,15	2,48	5,02	0,53	-	-	14,18
Immature bull (1–2yrs)	5,04	2,86	6,66	0,43	-	-	14,99	5,82	2,30	6,66	0,50	-	-	15,28	6,56	2,70	6,66	0,56	-	-	16,48
Sub-adult cow (2–3yrs)	6,53	4,03	1,28	0,56	-	-	12,40	6,71	2,78	1,28	0,57	-	-	11,34	6,88	2,88	1,28	0,59	-	-	11,63
Sub-adult bull (2–3yrs)	7,14	4,54	4,21	0,61	-	-	16,50	7,64	3,31	4,21	0,65	-	-	15,81	8,11	3,58	4,21	0,69	-	-	16,59
Adult, non-pregnant cow	6,97	4,39	-	0,60	-	-	11,96	6,97	2,93	-	0,60	-	-	10,50	6,97	2,69	-	0,60	-	-	10,26
Adult, lactating pregnant cow	8,08	5,35	-	0,69	1,90	18,57	34,59	7,16	3,04	-	0,61	0,01	26,15	36,97	7,53	3,25	-	0,65	3,63	8,93	23,99
Lone, territorial bull	8,32	5,57	-	0,71	-	-	14,60	8,32	3,71	-	0,71	-	-	12,74	8,32	3,71	-	0,71	-	-	12,74
Adult, mixed herd bull	8,56	5,78	-	0,73	-	-	15,07	8,56	3,86	-	0,73	-	-	13,15	8,56	3,86	-	0,73	-	-	13,15
Adult, bachelor herd bull	8,80	6,00	-	0,75	-	-	15,55	8,80	4,00	-	0,75	-	-	13,55	8,80	4,00	-	0,75	-	-	13,55

Appendix 11 : Seasonal protein budget in individual wildebeest and the population at Etosha (1978)

	Protein requirements (kg DM)								
	Wet, hot season (Jan. to April)			Dry, cold season (May to Aug.)			Dry, hot season (Sept. to Dec.)		
Age-sex and social class	Budget of the individual	Mean no. of individuals	Budget of the population	Budget of the individual	Mean no. of individuals	Budget of the population	Budget of the individual	Mean no. of individuals	Budget of the population
Calves (0-1yr)	7,958	678	5 396	9,302	537	4 995	10,530	395	4 159
Immature cow (1 - 2 yrs)	9,930	159	1 579	10,194	150	1 529	10,812	142	1 535
Immature bull (1 - 2 yrs)	11,243	155	1 743	11,747	138	1 621	12,566	120	1 508
Sub-adult cow (2 - 3 yrs)	9,300	134	1 246	8,718	128	1 116	8,868	122	1 082
Sub-adult bull (2 - 3 yrs)	12,375	106	1 312	12,154	94	1 142	12,650	82	1 037
Adult, non-pregnant cow	8,970	75	673	8,072	75	605	7,823	75	587
Adult, lactating, pregnant cow	25,943	748	19 405	28,421	748	21 259	18,292	748	13 682
Lone, territorial bull	10,950	175	1 916	9,794	150	1 469	9,714	50	486
Adult, mixed herd bull	11,303	100	1 130	10,109	100	1 011	10,027	100	1 003
Adult, bachelor herd bull	11,663	324	3 779	10,417	349	3 636	10,332	449	4 639
Seasonal totals	-	2 454	38 179	-	2 269	38 383	-	2 083	29 718
Yearly total	106 280								

Appendix 12 : Grasses eaten by wildebeest and areas of dominant occurrence at Etosha

Grass species	Annual, (A) Biennial (B) or Perennial (P)	Area of dominant occurrence						
		Grootvlakte	Okondeka	Ombika	Etosha Pan	Charitsaub	Chudop	Andoni
Antephora pubescens +	P							
A. schinzii	A		X	X				
Cenchrus ciliaris ++	P	X						
Chloris virgata ++	A						X	
Cynodon dactylon	P							X
Dactyloctenium aegyptium ++	A							X
Enneapogon brachystachyus ++	A/B	X	X	X		X	X	
Eragrostis annulata ++	A	X	X	X		X		X
E. nindensis ++	P	X	X	X		X	X	
E. echinochloidea ++	P	X	X			X		
E. glandulosipedata	A	X		X				
E. rotifer +	P							
E. sabinae	P	X	X					
Monelytrum luederitzianum ++	P	X	X	X		X	X	X
Odyssea paucinervis ++	P		X			X	X	X
Oropetium capense	A/B	X		X				
Panicum lanipes	P		X	X				
Sporobolus acinifolius	P		X			X		
S. tenellus	P				X			
S. spicatus ++	P		X			X		
Stipagrostis uniplumis +	P							
Tragus berteronianus +	A							
T. racemosus ++	A	X	X			X		X
Urochloa brachyura	A	X						X

+ Tinley (1967)
++ Tinley (1967) and present study

Appendix 13 : Moisture content of wildebeest food species at Etosha during 1976

Area	Stage of grass growth	Percentage moisture ($^{w}/w$)			Ambient conditions			
					Relative humidity (%)		Temperature (°C)	
		Range of 10 replicates	Mean	Standard deviation	Range of 10 replicates	Mean	Range of 10 replicates	Mean
Grootvlakte	sprouting	71,1 - 77,1	74,4	1,8	56 - 76	63	24,8 - 28,1	26,5
	seeding	48,5 - 62,7	58,1	4,0	41 - 76	51	24,6 - 31,1	28,6
	dormant	3,3 - 55,7	4,9	0,7	24 - 25	24	13,7 - 24,6	19,8
Okondeka	sprouting	64,4 - 72,5	69,4	2,6	53 - 80	71	23,8 - 27,1	25,1
	seeding	58,7 - 70,8	63,5	3,4	67 - 95	83	19,3 - 24,7	21,4
	dormant	3,4 - 8,2	5,7	1,3	22 - 24	23	24,7 - 28,8	26,8
Ombika	sprouting	67,2 - 76,5	71,7	2,4	62 - 76	70	23,2 - 26,1	25,0
	seeding	59,2 - 68,9	63,2	3,2	40 - 46	44	30,8 - 32,5	31,5
	dormant	3,5 - 4,6	4,1	0,3	18 - 20	19	28,8 - 31,4	30,2
Charitsaub	sprouting	76,1 - 84,4	79,5	2,9	67 - 84	79	21,2 - 25,3	22,9
	seeding	61,3 - 66,8	64,3	1,8	58 - 83	71	22,9 - 27,7	24,4
	dormant	3,6 - 5,0	4,4	0,4	20 - 23	21	23,3 - 26,1	24,2
Chudop	sprouting	66,0 - 78,6	69,1	3,9	43 - 55	50	29,1 - 32,2	30,4
	seeding	60,3 - 81,3	68,1	6,6	78 - 92	84	20,6 - 25,2	23,2
	dormant	4,5 - 12,0	8,5	2,4	20 - 25	21	28,3 - 31,4	29,7
Andoni	sprouting	72,1 - 81,5	77,2	3,1	50 - 71	60	25,6 - 29,1	27,7
	seeding	55,2 - 59,6	57,1	1,3	47 - 70	59	27,0 - 29,8	28,3
	dormant	3,2 - 11,1	6,4	2,4	23 - 26	24	29,7 - 31,9	31,0
Etosha Pan	seeded	20,1 - 38,6	29,4	5,8	23 - 28	26	30,0 - 31,1	30,6
	dormant	3,5 - 4,8	4,1	0,4	16 - 22	20	25,3 - 28,9	26,7

Appendix 14 : Moisture content and proximate analyses of wildebeest faeces, on a seasonal basis, at Etosha (1976 - 78)

Season	Age-sex and social class	Moisture in fresh faeces (%)	Component (% of dry matter)					Gross energy value (kJ.g^{-1})
			Crude protein	Fat	Soluble carbo-hydrates (NFE)	Crude fibre	Ash	
Wet, hot (Jan. to April)	**Cows:**							
	1 month old calf	74,50	9,0	2,7	42,8	17,4	28,1	19,35
	1 year old	78,03	10,5	2,8	31,0	23,3	24,7	18,06
	2 years old	65,72	10,7	3,5	40,3	19,5	26,0	17,30
	3 years old	68,15	7,9	2,0	40,9	24,4	24,8	16,50
	adult, non-lactating	79,32	9,2	3,8	37,4	27,4	22,2	19,10
	adult, lactating	77,08	10,4	3,7	33,0	28,5	24,4	19,67
	" "	74,72	12,2	3,6	31,5	21,9	30,8	18,70
	" "	75,34	8,3	3,6	34,8	25,7	27,6	16,96
	Bulls:							
	1 year old, mixed herd	79,46	9,4	2,7	40,8	18,8	28,3	13,60
	2 years old, mixed herd	75,40	9,2	3,2	38,3	26,8	22,5	21,60
	adult, territorial, mixed herd	74,43	9,9	2,8	41,5	20,2	25,6	18,55
	lone territorial	79,73	8,9	2,8	38,7	24,0	25,6	18,53
	" "	73,81	9,1	2,7	35,4	29,6	23,2	20,03
	" "	69,52	7,4	2,0	41,4	23,3	25,9	18,80
	" "	-	11,1	3,4	36,5	24,9	24,1	19,55
	" "	70,29	9,0	2,6	42,4	21,7	24,3	-
	" "	66,67	8,3	2,0	42,0	19,9	27,8	15,53
	" "	82,40	8,6	3,2	34,8	29,6	23,8	18,90
	" "	76,53	8,8	3,6	33,7	29,1	24,8	19,76
	" "	67,84	6,9	2,0	32,9	21,3	36,9	13,80
	adult, bachelor herd	69,77	8,7	1,6	41,5	19,4	28,8	15,20
	" "	69,39	7,8	2,2	44,6	21,6	23,8	16,63
	" "	70,24	6,6	2,0	44,4	22,0	25,0	15,23
	" "	52,29	7,4	2,5	39,4	24,7	26,0	14,53
Mean ± SD		72,64 ± 6,43	9,0 ± 1,4	2,8 ± 0,7	38,3 ± 4,1	23,5 ± 3,6	26,0 ± 3,1	17,65 ± 2,18

Appendix 14 : (continued)

Season	Age-sex and social class	Moisture in fresh faeces (%)	Component (% of dry matter)					Gross energy value (kJ.g⁻¹)
			Crude protein	Fat	Soluble carbo-hydrates (NFE)	Crude fibre	Ash	
Dry, cold (May to August)	**Cows:**							
	3 months old calf, abandoned	67,92	11,3	2,9	41,2	22,9	21,7	17,65
	1½ year old	66,63	7,8	2,4	47,6	25,1	17,1	20,67
	1½ " "	68,19	9,0	2,4	40,9	26,7	21,0	16,75
	1½ " "	72,19	11,5	2,4	40,8	26,8	18,5	20,83
	adult, non-lactating, pregnant	73,74	16,8	2,4	55,7	16,5	8,6	19,95
	adult, lactating	72,39	8,7	2,4	42,0	27,2	19,7	18,40
	" "	68,08	9,7	2,4	48,7	22,1	17,1	16,80
	" "	68,67	8,7	2,4	47,4	20,7	20,8	17,23
	" "	68,27	8,3	2,1	42,4	24,0	23,2	16,85
	" "	70,73	8,0	2,4	41,0	25,5	23,1	17,15
	" "	65,78	7,8	2,3	46,8	23,8	19,3	16,96
	" "	74,17	11,4	2,3	47,2	17,6	21,5	15,85
	Bulls:							
	1½ year old, mixed herd	67,92	9,2	2,5	45,6	23,3	19,4	19,85
	1½ " " " "	69,49	10,1	2,6	48,2	21,1	17,0	16,55
	1½ " " " "	64,03	9,1	2,4	46,3	21,9	20,3	16,67
	1½ " " " "	72,61	16,0	2,4	50,8	14,9	15,9	16,20
	1½ " " " "	67,99	9,4	2,9	44,8	22,5	20,4	16,76
	1½ " " " "	62,81	8,4	2,1	47,6	20,1	21,8	17,15
	1½ " " " "	72,45	14,0	1,9	48,4	17,7	18,0	–
	adult, territorial, mixed herd	67,96	8,2	2,4	43,3	25,3	20,8	16,00
	lone, territorial	65,39	5,8	2,4	47,8	26,9	17,1	17,30
	" "	68,05	5,9	2,4	45,0	25,1	21,6	18,13
	" "	66,08	6,4	2,4	50,3	23,9	17,0	16,30
	" "	70,07	6,7	2,4	52,8	21,0	17,1	15,50
	" "	–	15,0	3,3	45,8	21,5	14,4	20,70
	" "	–	16,6	2,4	53,7	22,0	5,3	22,50
	" "	–	12,2	2,4	47,9	25,2	12,3	23,20
	" "	–	13,3	2,5	49,2	22,6	12,4	21,76
	" "	–	11,9	2,2	44,8	30,1	11,0	22,35
	" "	65,60	8,9	2,7	46,1	22,4	19,9	19,80
	" "	71,80	16,6	2,1	52,8	16,9	11,6	18,55
Mean ± SD		68,81 ± 3,01	10,4 ± 3,3	2,4 ± 0,3	46,9 ± 3,9	22,7 ± 3,5	17,6 ± 4,3	18,35 ± 2,23

Appendix 14 : (continued)

Season	Age-sex and social class	Moisture in fresh faeces (%)	Component (% of dry matter)					Gross energy value (kJ.g^{-1})
			Crude protein	Fat	Soluble carbohydrates (NFE)	Crude fibre	Ash	
Dry, hot (Sept. to December)	**Cows:**							
	6 months old calf	62,03	8,6	1,7	46,3	19,3	24,1	16,55
	2 years old	63,13	7,2	2,5	45,8	20,8	23,7	17,10
	adult, non-lactating, pregnant	63,31	7,3	2,4	45,9	19,2	25,0	15,80
	" " " "	59,48	7,9	2,5	44,1	20,5	25,0	-
	Bulls:							
	lone, territorial	63,12	7,7	3,1	45,2	23,8	20,2	17,45
	" "	62,44	8,1	2,8	33,9	19,8	35,4	16,00
	" "	64,62	7,0	2,3	44,3	23,0	23,4	-
	adult, bachelor herd	70,42	8,4	2,5	45,0	19,1	25,0	15,20
	adult, bachelor herd	64,28	8,2	2,2	46,5	21,1	22,0	16,63
Mean ± SD		63,65 ± 2,94	7,8 ± 0,6	2,4 ± 0,4	44,1 ± 3,9	20,7 ± 1,7	24,9 ± 4,3	16,39 ± 0,78

Appendix 15 : Rumen contents of wildebeest at Etosha, sampled during two critical seasons (1978)

Season	Age - sex and social class	Number of grass components					Unidentifiable or non - grass
		Leaf	Sheath	Stem	Inflorescence	Roots	
Wet, hot (March)	1 month old cow calf	41	27	17	9	1	5
	1 year old cow	33	41	12	8	-	6
	1 year old bull	39	39	15	5	-	2
	2 year old cow	40	33	18	6	-	3
	2 year old bull	42	40	10	6	-	2
	adult, non - lactating cow	41	32	17	8	-	2
	adult, lactating cow	42	38	10	8	-	2
	lone, territorial bull	49	26	14	8	-	3
Mean ± SD		40,9 ± 4,4	34,5 ± 5,9	14,1 ± 3,2	7,3 ± 1,4	0,1	3,1 ± 1,6
Dry, hot (November)	8 month old cow	15	38	40	3	1	6
	8 month old bull	3	24	63	3	2	5
	20 month old cow	4	14	70	9	-	3
	20 month old bull	4	23	68	4	-	1
	adult, pregnant cow	5	27	61	1	1	5
	adult, pregnant cow	-	8	74	9	-	9
	adult, lactating cow	8	38	48	1	-	1
	adult, bachelor bull	5	24	68	2	-	1
Mean ± SD		5,5 ± 4,4	24,5 ± 10,4	61,5 ± 11,7	4,0 ± 3,3	0,6	3,9 ± 2,9

Appendix 16 : Yields of grass and removal by large herbivores in the wet season grazing areas of Etosha, expressed as dry mass. 1972 - 1977 data from le Roux (1979), 1978 data from present study.

Area	Seasonal year and no. of replicates	Mean yield ($g.m^2$)		Grass removed		Total yield (area x $kg.ha^{-1}$)	Total removal (area x $kg.ha^{-1}$)	Percentage utilisation
		protected	residue after grazing	$g.m^2$	$kg.ha^{-1}$			
Grootvlakte - Okondeka (102 000 ha)	1972 (n = 49)	22,26	19,02	3,24	32,4	22 705 200	3 304 800	14,6
	1973 (n = 47)	30,66	22,55	8,11	81,1	31 273 200	8 272 200	26,5
	1974 (n = 31)	107 70	90,70	17,00	170,0	109 854 000	17 340 000	15,8
	1975	no data collected						
	1976 (n = 32)	118,09	85,39	32,70	327,0	120 451 800	33 354 000	27,7
	1977 (n = 34)	17,30	15,70	1,60	16,0	17 646 000	1 632 000	9,3
	1978 (n = 45)	69,17	46,94	22,23	222,3	70 553 400	22 674 600	32,1
Mean ± SD		60,86 ± 44,35	46,72 ± 33,90	14,15 ± 12,09	141,5 ± 120,9	59 433 700 ± 48 696 580	14 429 600 ± 12 329 126	21,0 ± 9,0

Appendix 16 : (continued)

Area	Seasonal year & no. of replicates	Mean yield (g.m^{2})		Grass removed		Total yield (area x kg.ha^{-1})	Total removal (area x kg.ha^{-1})	Percentage utilisation
		protected	residue after grazing	g.m^{2}	kg.ha^{-1}			
Chudop (6 300 ha)	1972 (n = 10)	46,70	19,03	27,62	276,2	2 942 100	1 740 060	59,2
	1973 (n = 7)	36,82	11,78	25,04	250,4	2 319 660	1 577 520	68,0
	1974 (n = 9)	142,27	22,93	119,34	1 193,4	8 963 010	7 518 420	83,9
	1975	no data collected						
	1976 (n = 7)	124,69	40,99	83,70	837,0	7 855 470	5 273 100	67,1
	1977 (n = 9)	64,29	21,93	42,36	423,6	4 050 270	2 668 680	65,9
	1978 (n = 10)	96,53	36,56	59,97	599,7	6 081 390	3 778 110	62,1
Mean ± SD		85,22 ± 42,91	25,55 ± 11,05	59,67 ± 36,51	596,7 ± 365,1	5 368 650 ± 2 703 121	3 759 315 ± 2 299 995	67,7 ± 8,6

Appendix 17 : Yields of grass and removal by large herbivores in the dry season grazing areas of Etosha, expressed as dry mass. 1973 - 77 data from le Roux (1979), 1978 data from present study.

Area	Seasonal year & no. of replicates	Mean yield (g.m^{2})		Grass removed		Total yield (area x kg.ha^{-1})	Total removal (area x kg.ha^{-1})	Percentage utilisation
		protected	residue after grazing	g.m^{2}	kg.ha^{-1}			
Charitsaub (15 600 ha)	1973 (n = 20)	51,30	19,50	31,80	318,0	8 002 800	4 960 800	62,0
	1974 (n = 20)	140,97	88,18	52,79	527,9	21 991 320	8 235 240	37,4
	1975 (n = 20)	127,83	37,10	90,73	907,3	19 941 480	14 153 880	71,0
	1976 (n = 20)	116,90	50,50	66,40	664,0	18 236 400	10 358 400	56,8
	1977 (n = 20)	45,41	31,23	14,18	141,8	7 083 960	2 212 080	31,2
	1978 (n = 20)	46,10	12,94	33,16	331,6	7 191 600	5 172 960	71,9
Mean ± SD		88,09 ± 45,04	39,91 ± 27,09	48,18 ± 27,62	481,8 ± 276,2	13 741 260 ± 7 026 523	7 515 560 ± 4 308 328	55,1 ± 17,1
Andoni (4 400 ha)	1973 (n = 10)	60,86	43,44	17,42	174,2	2 677 840	766 480	28,6
	1974 (n = 13)	172,03	157,53	14,50	145,0	7 569 320	638 000	8,4
	1975 (n = 10)	195,59	80,29	115,30	1 153,0	8 605 960	5 073 200	59,0
	1976 (n = 17)	274,22	185,85	88,37	883,7	12 065 680	3 888 280	32,2
	1977 (n = 20)	166,07	115,26	50,81	508,1	7 307 080	2 235 640	30,6
	1978 (n = 20)	183,05	143,25	39,80	398,0	8 054 200	1 751 200	21,7
Mean ± SD		175,30 ± 68,48	120,94 ± 52,42	54,37 ± 40,12	543,7 ± 401,2	7 713 347 ± 3 013 233	2 392 133 ± 1 765 310	30,1 ± 16,6

Appendix 17 : (continued)

Area	Seasonal year & no. of replicates	Mean yield (g.m^2)		Grass removed		Total yield (area x kg.ha^{-1})	Total removal (area x kg.ha^{-1})	Percentage utilisation
		protected	residue after grazing	g.m^2	kg.ha^{-1}			
Gemsbokvlakte (13 800 ha)	1973 (n = 11)	33,90	20,10	13,80	138,0	4 678 200	1 904 400	40,1
	1974 (n = 11)	91,80	57,50	34,30	343,0	12 668 400	4 733 400	37,4
	1975 (n = 12)	106,24	no data collected					
	1976 (n = 18)	166,84	60,54	106,30	1 063,0	23 023 920	14 669 400	63,7
	1977 (n = 20)	38,90	31,37	7,53	75,3	5 368 200	1 039 140	19,4
	1978 (n = 20)	85,10	29,60	55,50	555,0	11 743 800	7 659 000	65,2
Mean ± SD		87,13 ± 48,79	39,82 ± 18,07	43,49 ± 39,84	434,9 ± 398,4	11 496 504 ± 7 388 525	6 001 068 ± 5 497 707	45,2 ± 19,3
Ombika (1 400 ha)	1978 (n = 20)	110,95	6,45	104,50	1 045,0	1 553 300	1 463 000	94,2
Etosha Pan (20 000 ha)	1978 (n = 20)	144,15	23,15	121,00	1 210,0	28 830 000	24 200 000	83,9

Appendix 18 : Maximum and residual yield of crude protein (CP) and metabolisable energy (ME) in grass produced by the wet season grazing areas of Etosha (1972 – 78)

Area	Seasonal year	Maximum grass yield (seeding)					Residual grass yield (dormant)				
		Mean CP content (%)	Mean ME (MJ.kg $^{-1}$)	Total mass (kg DM)	Total CP (kg DM)	Total ME (MJ)	Mean CP content (%)	Mean ME (MJ.kg $^{-1}$)	Total mass (kg DM)	Total CP (kg DM)	Total ME (MJ)
Grootvlakte – Okondeka (102 000 ha)	1972	9,52	11,0667	22 705 200	2 161 535	251 271 637	3,28	11,0191	19 400 400	636 333	213 774 948
	1973			31 273 200	2 977 209	346 091 122			23 001 000	754 433	253 450 319
	1974			109 854 000	10 458 101	1 215 721 262			92 514 000	3 034 459	1 019 421 017
	1975			No data collected					No data collected		
	1976			120 451 800	11 467 011	1 333 003 935			87 097 800	2 856 808	959 739 368
	1977			17 646 000	1 679 899	195 282 988			16 014 000	525 259	176 459 867
	1978			70 553 400	6 716 684	780 793 312			47 878 800	1 570 425	527 581 285
Chudop (6 300 ha)	1972	13,20	12,2992	2 942 100	388 357	36 185 476	6,03	12,3797	1 202 040	72 483	14 880 895
	1973			2 319 660	306 195	28 529 962			742 140	44 751	9 187 471
	1974			8 963 010	1 183 117	110 237 853			1 444 590	87 108	17 883 591
	1975			No data collected					No data collected		
	1976			7 855 470	1 036 922	96 615 997			2 582 370	155 717	31 968 966
	1977			4 050 270	534 636	49 815 081			1 381 590	83 310	17 103 670
	1978			6 081 390	802 743	74 796 232			2 303 280	138 888	28 513 915

Appendix 19 : Maximum and residual yield of crude protein (CP) and metabolisable energy (ME) in grass produced by the dry season grazing areas of Etosha (1973 – 78)

Area	Seasonal year	Maximum grass yield (seeding)					Residual grass yield (dormant)				
		Mean CP content (%)	Mean ME ($MJ.kg^{-1}$)	Total mass (kg DM)	Total CP (kg DM)	Total ME (MJ)	Mean CP content (%)	Mean ME ($MJ.kg^{-1}$)	Total mass (kg DM)	Total CP (kg DM)	Total ME (MJ)
Charitsaub (15 600 ha)	1973	10,23	11,2808	8 002 800	818 686	90 277 986	3,10	10,7944	3 042 000	94 302	32 836 565
	1974			21 991 320	2 249 712	248 079 683			13 756 080	426 438	148 488 630
	1975			19 941 480	2 040 013	224 955 848			5 787 600	179 419	62 473 669
	1976			18 236 400	1 865 584	205 721 181			7 878 000	244 218	85 038 283
	1977			7 083 960	724 689	79 912 736			4 871 880	151 028	52 589 021
	1978			7 191 600	735 701	81 127 001			2 018 640	62 578	21 790 008
Andoni (4 400 ha)	1973	8,43	11,4165	2 677 840	225 742	30 571 560	2,56	11,2974	1 911 360	48 931	21 593 398
	1974			7 569 320	638 094	86 415 142			6 931 320	177 442	78 305 895
	1975			8 605 960	725 482	98 249 942			3 532 760	90 439	39 911 003
	1976			12 065 680	1 017 137	137 747 836			8 177 400	209 341	92 383 359
	1977			7 307 080	615 987	83 421 279			5 071 440	129 829	57 294 086
	1978			8 054 200	678 969	91 950 774			6 303 000	161 357	71 207 512
Ombika (1 400 ha)	1978	7,83	11,1686	1 553 300	121 623	17 348 186	2,77	10,9690	90 300	2 501	990 501
Etosha Pan (20 000 ha)	1978	9,80	10,9856	28 830 000	2 825 340	316 714 848	7,76	11,2262	4 630 000	359 288	51 977 306

Appendix 20 : Detailed estimation of seasonal food intake by wildebeest at Etosha, based on the population structure during 1978

Age – sex and social class	Dry matter intake by season														
	Wet, hot season (Jan. to April)					Dry, cold season (May to Aug.)					Dry, hot season (Sept. to Dec.)				
	Mean body mass (kg)	Daily food intake (kg)	Mean number of individuals	Total daily food intake (kg)	Total seasonal food intake (kg)	Mean body mass (kg)	Daily food intake (kg)	Mean number of individuals	Total daily food intake (kg)	Total seasonal food intake (kg)	Mean body mass (kg)	Daily food intake (kg)	Mean number of individuals	Total daily food intake (kg)	Total seasonal food intake (kg)
Calves (0 – 1 yr)	33	0,99	678	671,22	80 546	61	1,22	537	555,14	80 582	90	1,80	395	711,00	86 742
Immature cows (1 – 2 yrs)	117	3,51	159	558,09	66 971	136	2,72	150	408,00	50 184	155	3,10	142	440,20	53 704
Immature bulls (1 – 2 yrs)	119	3,57	155	553,35	66 402	144	2,88	138	397,44	48 885	169	3,38	120	405,60	49 483
Sub – adult cows (2 – 3 yrs)	168	5,04	134	675,36	81 043	174	3,48	128	445,44	54 789	180	3,60	122	439,20	53 582
Sub – adult bulls (2 – 3 yrs)	189	5,67	106	601,02	72 122	207	4,14	94	389,16	47 867	224	4,48	82	367,36	44 818
Adult, non – pregnant cows	183	5,49	75	411,75	49 410	183	3,66	75	274,50	33 764	183	3,36	75	252,00	30 744
Adult, lactating & pregnant cows	223	6,69	748	5 004,12	600 494	190	3,80	748	2 842,40	349 615	203	4,06	748	3 036,88	370 499
Lone, territorial bulls	232	6,96	175	1 218,00	146 160	232	4,64	150	696,00	85 608	232	4,64	50	232,00	28 304
Adult bulls in mixed herds	241	7,23	100	723,00	86 760	241	4,82	100	482,00	59 286	241	4,82	100	482,00	58 804
Adult bulls in bachelor herds	250	7,50	324	2 430,00	291 600	250	5,00	349	1 745,00	214 635	250	5,00	449	2 245,00	273 890
Seasonal totals			2 454	12 845,91	1 541 508			2 269	8 335,08	1 025 215	-		2 083	8 611,24	1 050 570
Yearly total	3 617 293														

Appendix 21 : Occurrence of bacteria in water sampled from three types of drinking water available to wildebeest at Etosha (1974 - 78), according to Winter et al. (1979)

Origin of water	Year	Season	Mean bacterial counts (n = number of samples)										+ Relative drinking frequency by wildebeest
			Total plate counts/ml	n	Total coliforms /100 ml	n	Faecal coliforms /100 ml	n	Clostridia perfringens /100 ml	n	Enterococcal forms/100 ml	n	
Boreholes	1974	Dry	2 903	5	117	4	66	5	883	5	-	-	1
	1975	Dry	1 162	5	456	5	128	5	88	5	-	-	
	1975	Dry	23 751	12	8 096	13	4 493	13	236	13	-	-	
	1977	Wet	11 221	27	676	14	59	27	588	27	211	27	
	1977	Dry	25 549	30	1 377	28	212	28	1 644	30	599	30	
	1978	Wet	15 382	30	543	29	89	29	750	30	230	30	
	1978	Dry	59 806	32	2 089	30	1 151	32	644	32	322	32	
Artesian wells	1974	Dry	6 600	2	4 165	2	1 610	2	260	1	-	-	1
	1975	Dry	495	2	200	2	20	1	95	2	-	-	
	1975	Dry	735	2	<10	2	<10	2	715	2	-	-	
	1977	Wet	2 225	4	115	4	50	4	1 168	4	700	4	
	1977	Dry	15 020	4	175	4	47	3	335	4	191	4	
	1978	Wet	4 800	1	0	1	0	1	460	1	140	1	
	1978	Dry	12 257	3	10	3	4	3	73	3	72	3	
Fountains	1974	Dry	7 577	21	3 091	17	2 820	13	3 560	21	-	-	3
	1975	Dry	2 483	11	993	9	79	10	183	11	-	-	
	1975	Dry	8 742	19	7 005	18	5 887	19	2 599	19	-	-	
	1977	Wet	4 753	34	383	28	271	34	1 015	34	467	34	
	1977	Dry	10 388	33	1 546	31	331	30	2 044	32	714	30	
	1978	Wet	28 306	29	3 139	23	836	28	871	28	369	29	
	1978	Dry	38 962	33	1 743	29	961	26	698	33	386	33	

\+ 0 = not utilised
1 = seldom utilised (< 5 % of observations)
2 = infrequently utilised (<25 % of observations)
3 = commonly utilised (<50 % of observations)
4 = utilised exclusively when available

Appendix 22 : Occurrence of macro - elements in water sampled from five sources available to wildebeest at Etosha (1976 - 78), according to Dept. of Water Affairs (1977) and Winter <u>et al</u>. (1979). The relative drinking frequency of wildebeest was determined as given in Appendix 21.

Origin of water and number of samples	Season	Mean amount of macro - elements (mg/l)														pH	Conductivity (umho. cm $^{-1}$)	Relative drinking frequency by wildebeest
		TDS	SO_4	NO_3-N	F	Na	K	Ca	Mg	Cl	Si O_2	NO_2-N	Total alkalinity	NH_4-N	PO_4-P			
Boreholes (n = 33 - 36)	Dry	1 615	193	12,2	1,8	416	9	70	70	437	50	0	510	0,15	0	7,9	2 730	1
	Wet	1 778	267	7,0	1,6	492	9	70	71	551	42	0	434	0	0	7,8	2 886	
Artesian wells (n = 2)	Dry	15 233	1 500	0	4,5	5 754	67	21	27	6 500	22	0	1 553	0	0	9,0	23 625	1
Fountains (n = 28 - 33)	Dry	3 055	389	3,3	1,9	919	17	48	74	987	36	0,27	742	0	0,04	8,1	4 961	3
	Wet	2 380	349	1,6	1,3	773	28	56	51	741	33	0	564	0,40	0,19	7,9	4 144	
Ekuma River (n = 4)	Dry	39 493	2 450	0,5	3,6	14 955	420	-	-	18 867	15	0	2 786	-	-	9,6	57 750	1
	Wet	17 846	1 320	0	6,0	7 100	76	0	0	9 000	6	0	1 583	0	trace	10,0	2 554	
Rainwater pools (n = 5)	Wet	504	90	2,1	0,4	159	11	27	21	113	13	0	143	0	0	8,2	76	4

Appendix 23 : Occurrence of trace elements in water sampled from five sources available to wildebeest at Etosha (1976 – 78), according to Winter _et al_. (1979). The relative drinking frequency of wildebeest was determined as given in Appendix 21.

Origin of water and number of samples	Season	Mean amount of trace elements (ug/l)															Relative drinkin frequency by wildebeest
		Li	Aℓ	Cd	Co	Cr	Cu	Fe	Mn	Ni	Pb	Sr	Zn	Br	I	B	
Boreholes (n = 32 – 37)	Dry	<80	<100	<10	<50	<50	<50	<50	<25	<50	<100	1 290	380	1 070	112	410	1
	Wet	<70	<100	<10	<50	<50	<45	<390	<25	<50	<100	1 420	690	1 180	99	400	
Artesian wells (n = 2)	Dry	240	<100	<15	<70	<70	180	<50	<25	<70	<130	3 033	110	12 500	269	2 190	1
Fountains (n = 28 – 32)	Dry	<130	<100	<10	<50	<50	<70	<40	<30	<50	<100	1 220	<60	2 010	120	790	3
	Wet	<100	<100	<10	<50	<50	<45	<290	<45	<50	<100	1 190	580	1 450	<124	750	
Ekuma River (n = 1)	Wet	20	500	50	175	50	40	210	25	60	120	270	<25	1 680	110	4 400	1
Rainwater pools (n = 5)	Wet	40	<240	<10	<50	<120	<25	<130	<85	<50	<100	540	<25	80	<50	260	4

Appendix 24 : Detailed estimation of seasonal faecal production by wildebeest at Etosha, based on the population structure during 1978

Age – sex and social class	Dry matter faecal production by season														
	Wet, hot season (Jan. to Apr.)					Dry, cold season (May to Aug.)					Dry, hot season (Sept. to Dec.)				
	Mean body mass (kg)	Daily faecal production (kg)	Mean number of individuals	Total daily faecal production (kg)	Total seasonal faecal production (kg)	Mean body mass (kg)	Daily faecal production (kg)	Mean number of individuals	Total daily faecal production (kg)	Total seasonal faecal production (kg)	Mean body mass (kg)	Daily faecal production (kg)	Mean number of individuals	Total daily daily production (kg)	Total seasonal faecal producti (kg)
Calves (0 – 1 yr)	33	1,21	678	820,38	98 446	61	1,48	537	794,76	97 755	90	1,65	395	651,75	79 514
Immature cows (1 – 2 yrs)	117	1,76	159	297,84	33 581	136	1,83	150	274,50	33 764	155	1,89	142	268,38	32 742
Immature bulls (1 – 2 yrs)	119	1,77	155	274,35	32 922	144	1,85	138	255,30	31 402	169	1,92	120	230,40	28 109
Sub – adult cows (2 – 3 yrs)	168	1,92	134	257,28	30 874	174	1,94	128	248,32	30 543	180	1,95	122	237,90	29 024
Sub – adult bulls (2 – 3 yrs)	189	1,97	106	208,82	25 058	207	2,01	94	188,94	23 240	224	2,05	82	168,10	20 508
Adult, non – pregnant cows	183	1,96	75	147,00	17 640	183	1,96	75	147,00	18 081	183	1,96	75	147,00	17 934
Adult, lactating and pregnant cows	223	2,04	748	1 525,92	183 110	190	1,97	748	1 473,56	181 248	203	2,00	748	1 496,00	182 512
Lone, territorial bulls	232	2,06	175	360,50	43 260	232	2,06	150	309,00	38 007	232	2,06	50	103,00	12 566
Adult bulls in mixed herds	241	2,08	100	208,00	24 960	241	2,08	100	208,00	25 584	241	2,08	100	208,00	25 376
Adult bulls in bachelor herds	250	2,09	324	677,16	81 259	250	2,09	349	729,41	89 717	250	2,09	449	938,41	114 486
Seasonal totals			2 454	4 759,25	571 110			2 269	4 628,79	569 341			2 083	4 448,94	542 771
Yearly total	1 683 222														

Appendix 25 : Aerial counts of the five major competitors of wildebeest at Etosha (1968 - 78).
Corrected values to compensate for undercounting bias are bracketted.
Data for 1968 - 70 from Ebedes et al. (1970); for 1972 - 73 from Joubert et al. (1973); for 1974 - 78 from the present study.

Year	Month and season	Method	Species				
			Burchell's zebra	Springbok	Gemsbok	Red hartebeest	Ostrich
1968	September (dry, hot)	Fixed-wing aircraft (Fwa)	9 317 (18 073)	1 422 (3 364)	1 199 (1 902)	72 (124)	188 (316)
1969	April (wet, hot)	Fwa	11 488 (22 284)	6 488 (15 531)	2 328 (3 692)	55 (95)	856 (1 437)
1970	February (wet, hot)	Fwa	7 274 (14 110)	4 181 (9 892)	1 582 (2 509)	51 (88)	1 658 (2 784)
1972	October (dry, hot)	Fwa	8 468 (16 426)	2 969 (7 025)	1 719 (2 726)	64 (110)	468 (786)
1973	February (wet, hot)	Fwa	5 281 (10 244)	3 167 (7 493)	713 (1 131)	55 (95)	359 (603)
1973	March (wet, hot)	Fwa	7 760 (15 053)	4 445 (10 517)	1 743 (2 764)	80 (138)	1 073 (1 802)
1973	September (dry, hot)	Helicopter (H)	11 395 (13 902)	4 951 (8 367)	1 804 (2 201)	76 (128)	563 (822)
1974	July (dry, cold)	H	13 116 (16 002)	5 799 (9 800)	1 706 (2 081)	99 (167)	484 (707)
1976	July (dry, cold)	H	9 045 (11 035)	9 771 (16 411)	739 (902)	61 (103)	457 (667)
1977	March (wet, hot)	H	7 716 (9 414)	18 635 (31 493)	1 022 (1 247)	43 (73)	837 (1 222)
1978	September (dry, hot)	H	7 513 (9 166)	18 980 (32 076)	526 (642)	76 (128)	496 (724)

Appendix 26 : Detailed estimation of yearly, individual energy budgets for five major competitors of wildebeest at Etosha.

Resting metabolic rate was calculated as 70 $W_{kg}^{0,75}$ for mammals and 78,3 $W_{kg}^{0,723}$ for ostrich.

The energetic cost of egg production and incubation was added to the increment over resting metabolic rate of 1,9 in the case of adult ostrich cocks and hens (explanation given in the text).

Species	Increment over RMR	Age and sex class	Mean body mass (kg)	Energy requirements	
				kJ. day $^{-1}$	kJ. year $^{-1}$
Burchell's zebra	2,0	0 – 1 yr	158	26 104,31	9 528 073
		1 – 2 yrs	235	35 157,69	12 832 557
		Full-grown female	335	45 867,31	16 741 568
		FG male	318	44 110,32	16 100 268
Springbok	2,31	0 – 1 yr	20	6 398,42	2 335 425
	2,10	1 – 2 yrs	30	7 884,08	2 877 689
	1,91	FG female	37	8 392,18	3 063 147
	1,56	FG male	42	7 537,94	2 751 347
Gemsbok	2,31	0 – 1 yr	65	15 487,70	5 653 012
	2,10	1 – 2 yrs	140	25 032,54	9 136 877
	1,91	FG female	220	31 955,09	11 663 609
	1,56	FG male	240	27 859,46	10 168 702
Red hartebeest	2,31	0 – 1 yr	50	12 271,24	4 643 254
	2,10	1 – 2 yrs	115	21 598,94	7 883 612
	1,91	FG female	160	25 165,92	9 185 562
	1,56	FG male	180	22 452,72	8 195 245
Ostrich	1,9	0 – 2 yrs	60	12 014,63	4 385 340
		FG female	115	19 230,54	7 019 149
		FG male	120	19 831,48	7 238 489

Appendix 27 : Estimation of yearly energy budgets for the Burchell's zebra population on the grasslands of Etosha (1973 - 78)

Year	Estimated population	Age and sex class	Estimated number of individuals	Total energy requirements (kJ. year $^{-1}$)	
				Age and sex class	Population
1973	13 902	0 - 1 yr	1 501	14 301 637 573	
		1 - 2 yrs	1 126	14 449 459 182	
		Full - grown female	5 987	100 231 767 616	
		FG male	5 288	85 138 217 184	214 121 081 555
1974	16 002	0 - 1 yr	1 728	16 464 510 144	
		1 - 2 yrs	1 296	16 330 993 872	
		FG female	6 891	115 366 145 088	
		FG male	6 087	98 002 331 316	246 163 980 420
1975	13 519	0 - 1 yr	1 460	13 910 986 580	
		1 - 2 yrs	1 095	14 051 649 915	
		FG female	5 822	97 469 408 896	
		FG male	5 142	82 787 578 056	208 219 623 447
1976	11 035	0 - 1 yr	1 192	11 357 472 485	
		1 - 2 yrs	894	11 472 314 440	
		FG female	4 752	79 555 935 432	
		FG male	4 197	67 572 800 118	169 958 522 475
1977	9 414	0 - 1 yr	1 017	9 690 058 320	
		1 - 2 yrs	762	9 778 415 664	
		FG female	4 054	67 870 320 337	
		FG male	3 581	57 655 038 652	144 993 832 973
1978	9 166	0 - 1 yr	990	9 432 800 135	
		1 - 2 yrs	742	9 521 764 334	
		FG female	3 947	66 078 972 464	
		FG male	3 487	56 141 614 012	141 175 150 945

Appendix 28 : Estimation of yearly energy budgets for the springbok population on the grasslands of Etosha (1973 - 78)

Year	Estimated population	Age and sex class	Estimated number of individuals	Total energy requirements (kJ. year $^{-1}$)	
				Age and sex class	Population
1973	8 367	0 - 1 yr	1 933	4 514 376 525	
		1 - 2 yrs	661	1 902 152 429	
		Full - grown female	3 481	10 662 814 707	
		FG male	2 292	6 306 087 324	23 385 430 985
1974	9 800	0 - 1 yr	2 264	5 287 411 944	
		1 - 2 yrs	774	2 227 327 472	
		FG female	4 077	12 488 438 316	
		FG male	2 685	7 387 347 427	27 390 525 159
1975	13 106	0 - 1 yr	3 028	7 071 679 933	
		1 - 2 yrs	1 035	2 978 403 015	
		FG female	5 453	16 703 324 537	
		FG male	3 590	9 877 309 968	36 630 717 453
1976	16 411	0 - 1 yr	3 791	8 853 612 491	
		1 - 2 yrs	1 296	3 729 478 557	
		FG female	6 828	20 915 147 614	
		FG male	4 496	12 370 023 849	45 868 262 511
1977	31 493	0 - 1 yr	7 275	16 990 248 187	
		1 - 2 yrs	2 488	7 159 677 971	
		FG female	13 103	39 872 784 566	
		FG male	8 627	23 735 870 569	87 758 581 293
1978	32 076	0 - 1 yr	7 410	17 305 531 143	
		1 - 2 yrs	2 534	7 292 051 438	
		FG female	13 346	40 880 720 571	
		FG male	8 786	24 173 271 694	89 651 574 846

Appendix 29 : Estimation of yearly energy budgets for the gemsbok population on the grasslands of Etosha (1973 -78)

Year	Estimated population	Age and sex class	Estimated number of individuals	Total energy requirements (kJ. year $^{-1}$)	
				Age and sex class	Population
1973	2 201	0 - 1 yr	172	972 318 064	
		1 - 2 yrs	196	1 790 827 892	
		Full - grown female	1 348	15 722 544 932	
		FG male	485	4 565 747 198	23 051 438 086
1974	2 081	0 - 1 yr	163	921 440 755	
		1 - 2 yrs	185	1 690 322 235	
		FG female	1 273	14 847 777 159	
		FG male	460	4 677 604 639	22 137 144 788
1975	1 492	0 - 1 yr	116	655 749 249	
		1 - 2 yrs	133	1 215 204 634	
		FG female	914	10 660 540 710	
		FG male	329	3 345 504 187	15 876 998 780
1976	902	0 - 1 yr	71	401 363 765	
		1 - 2 yrs	80	730 950 156	
		FG female	552	6 438 313 427	
		FG male	199	2 023 572 441	9 594 199 789
1977	1 247	0 - 1 yr	97	548 342 045	
		1 - 2 yrs	111	1 014 193 341	
		FG female	764	8 910 999 018	
		FG male	275	2 796 394 077	13 269 928 481
1978	642	0 - 1 yr	50	282 650 538	
		1 - 2 yrs	57	520 801 986	
		FG female	393	4 583 799 233	
		FG male	142	1 443 956 215	6 831 207 972

Appendix 30 : Estimation of yearly energy budgets for the red hartebeest population on the grasslands of Etosha (1973 - 78)

Year	Estimated population	Age and sex class	Estimated number of individuals	Total energy requirements (kJ. year $^{-1}$)	
				Age and sex class	Population
1973	128	0 - 1 yr	16	74 292 064	
		1 - 2 yrs	11	86 719 732	
		Full - grown female	54	496 020 348	
		FG male	47	385 176 515	1 042 208 659
1974	167	0 - 1 yr	21	97 508 216	
		1 - 2 yrs	14	110 370 598	
		FG female	71	652 175 197	
		FG male	61	499 909 546	1 359 963 557
1975	135	0 - 1 yr	17	78 935 223	
		1 - 2 yrs	11	86 719 756	
		FG female	57	523 577 271	
		FG male	50	409 761 923	1 098 994 173
1976	103	0 - 1 yr	13	60 362 229	
		1 - 2 yrs	8	63 068 913	
		FG female	44	404 164 911	
		FG male	38	311 419 061	839 015 114
1977	73	0 - 1 yr	9	41 789 236	
		1 - 2 yrs	6	47 301 685	
		FG female	31	284 752 551	
		FG male	27	221 127 144	594 970 616
1978	128	0 - 1 yr	16	74 292 064	
		1 - 2 yrs	11	86 719 732	
		FG female	54	496 020 348	
		FG male	47	385 176 515	1 042 208 659

Appendix 31 : Estimation of yearly energy budgets for the ostrich population on the grasslands of Etosha (1973 –78)

Year	Estimated population	Age and sex class	Estimated number of individuals			Total energy requirements (kJ. year $^{-1}$)			
			Egg – laying	Incubating	Total	Age and sex class			Population total
						Egg – laying	Incubating	Total	
1973	822	0 – 2 yrs	–	–	154	–	–	675 342 360	
		Full – grown female	296	99	329	25 299 712	2 028 510	2 336 628 243	
		FG male	–	99	339	–	2 873 970	2 456 721 747	5 468 692 350
1974	707	0 – 2 yrs	–	–	132	–	–	578 864 880	
		FG female	255	85	283	21 795 360	1 741 650	2 114 506 332	
		FG male	–	85	292	–	2 467 550	2 359 906 568	5 053 277 780
1975	687	0 – 2 yrs	–	–	128	–	–	561 323 520	
		FG female	248	83	276	21 197 056	1 700 670	2 062 146 959	
		FG male	–	83	283	–	2 409 490	2 287 187 717	4 910 658 196
1976	667	0 – 2 yrs	–	–	125	–	–	548 167 500	
		FG female	240	80	267	20 513 280	1 639 200	1 994 904 455	
		FG male	–	80	275	–	2 322 400	2 222 513 256	4 765 585 211
1977	1 222	0 – 2 yrs	–	–	229	–	–	1 004 242 286	
		FG female	441	147	490	37 693 152	3 012 030	3 661 111 428	
		FG male	–	147	503	–	4 267 410	4 065 198 322	8 730 552 036
1978	724	0 – 2 yrs	–	–	135	–	–	592 020 900	
		FG female	261	87	290	22 308 192	1 782 630	2 166 780 233	
		FG male	–	87	299	–	2 525 610	2 416 478 578	5 175 279 711

Appendix 32: Estimation of individual, daily nitrogen requirements in competitors of wildebeest at Etosha, on a seasonal basis. The calculation of RMR to estimate nitrogen requirements was taken at 70 $W_{kg}^{0,75}$ for mammals and 78,3 $_{kg}^{0,723}$ for ostrich. Explanation of the detailed requirements is given in the text.

Species	Age-sex class	Seasonal nitrogen requirements (g.day^{-1})																				
		Wet, hot (Jan. to April)							Dry, cold (May to Aug.)							Dry, hot (Sept. to Dec.)						
		Maintenance		Growth		Gestation (Qnp)	Lactation (Qnl)	Daily total	Maintenance		Growth		Gestation (Qnp)	Lactation (Qnl)	Daily total	Maintenance		Growth		Gestation (Qnp)	Lactation (Qnl)	Daily total
		EUN	MFN	Qng	Qnh				EUN	MFN	Qng	Qnh				EUN	MFN	Qng	Qnh			
Burchell's zebra	0-1 yr	3,74	1,12	11,90	0,32	-	-	13,38	5,27	1,51	11,90	0,45	-	-	19,13	7,16	2,78	11,90	0,61	-	-	22,41
	1-2 yrs	7,81	5,11	4,27	0,67	-	-	17,86	8,40	3,76	4,27	0,72	-	-	17,15	8,99	4,11	4,27	0,77	-	-	18,14
	Full-grown female	10,96	8,04	-	0,94	1,7	58,92	80,56	10,96	5,36	-	0,94	0,13	67,88	85,27	10,96	5,36	-	0,94	6,5	40,14	63,90
	FG male	10,54	7,63	-	0,90	-	-	19,07	10,54	5,09	-	0,90	-	-	16,53	10,54	5,09	-	0,90	-	-	16,53
Springbok	0-1 yr	0,84	0,15	2,03	0,11	-	-	3,13	1,32	0,24	2,03	0,19	-	-	3,79	1,73	0,64	2,03	0,24	-	-	4,64
	1-2 yrs	1,61	0,63	0,96	0,20	-	-	3,40	1,79	0,48	0,96	0,26	-	-	3,49	1,96	0,55	0,96	0,23	-	-	3,70
	FG female	2,10	0,89	-	0,30	0	8,57	11,86	2,10	0,59	-	0,30	0,01	5,57	8,56	2,10	0,59	-	0,30	0,73	-	3,34
	FG male	2,31	1,00	-	0,33	-	-	3,64	2,31	0,68	-	0,33	-	-	3,32	2,31	0,68	-	0,33	-	-	3,32
Gemsbok	0-1 yr	1,93	0,53	8,05	0,17	-	-	10,68	3,20	0,78	8,05	0,27	-	-	12,30	4,12	1,35	8,05	0,35	-	-	13,87
	1-2 yrs	5,24	2,80	4,61	0,43	-	-	13,08	5,70	2,24	4,61	0,49	-	-	13,04	6,97	2,62	4,61	0,56	-	-	14,76
	FG female	8,00	5,35	-	0,69	3,69	26,80	44,53	8,00	3,86	-	0,69	1,85	8,71	23,11	8,00	3,86	-	0,69	0,01	18,27	30,83
	FG male	8,54	5,78	-	0,73	-	-	15,05	8,54	4,00	-	0,73	-	-	13,30	8,54	4,00	-	0,73	-	-	13,30
Red hartebeest	0-1 yr	1,68	0,39	6,12	0,14	-	-	8,33	2,59	0,59	6,12	0,23	-	-	9,53	3,38	1,04	6,12	0,29	-	-	10,83
	1-2 yrs	4,27	2,28	3,93	0,36	-	-	10,84	4,93	1,84	3,93	0,42	-	-	11,01	5,57	2,16	3,93	0,40	-	-	12,06
	FG female	6,33	3,86	-	0,55	0,01	23,93	34,68	6,33	2,57	-	0,55	2,63	4,18	16,26	6,33	2,57	-	0,55	0	21,43	30,88
	FG male	6,87	4,30	-	0,58	-	-	11,75	6,84	2,87	-	0,58	-	-	10,29	6,84	2,87	-	0,58	-	-	10,29
Ostrich	0-2 yrs	3,02	0,96	4,68	0,77	-	-	9,43	3,02	1,44	4,68	0,77	-	-	9,91	3,02	1,44	4,68	0,77	-	-	9,91
	FG female	4,84	2,76	-	1,24	-	-	8,84	4,84	1,84	-	1,24	-	-	7,92	4,84	1,84	-	1,24	-	-	7,92
	FG male	4,99	2,88	-	1,27	-	-	9,14	4,99	1,92	-	1,27	-	-	8,18	4,99	1,92	-	1,27	-	-	8,18

Appendix 33 : Seasonal protein budgets for the Burchell's zebra population on the grasslands of Etosha (1973 - 78)

Year	Age-sex class	Population protein requirements (kg DM)						
		Seasonal totals						Yearly total
		Wet, hot season (Jan. to April)		Dry, cold season (May to Aug.)		Dry, hot season (Sept. to Dec.)		
		Class totals	Population total	Class totals	Population total	Class totals	Population total	
1973	0-1 yr	15 062	467 244	22 074	496 568	25 649	399 585	1 363 397
	1-2 yrs	15 083		14 845		15 575		
	Full-grown female	361 735		392 454		291 711		
	FG male	75 364		67 195		66 650		
1974	0-1 yr	17 340	538 112	25 412	571 558	29 528	459 932	1 569 602
	1-2 yrs	17 356		17 086		17 926		
	FG female	416 354		451 712		335 757		
	FG male	87 062		77 348		76 721		
1975	0-1 yr	14 651	454 630	21 471	482 884	24 948	388 575	1 326 089
	1-2 yrs	14 668		14 436		15 146		
	FG female	351 765		381 638		283 671		
	FG male	73 546		65 339		64 810		
1976	0-1 yr	11 962	371 083	17 530	384 145	20 369	317 170	1 072 398
	1-2 yrs	11 975		11 786		12 366		
	FG female	287 116		311 498		231 536		
	FG male	60 030		53 331		52 899		
1977	0-1 yr	10 206	316 575	14 956	336 250	17 378	270 580	923 405
	1-2 yrs	10 207		10 046		10 540		
	FG female	244 943		265 744		197 527		
	FG male	51 219		45 504		45 135		
1978	0-1 yr	9 935	306 227	14 559	327 381	16 917	263 444	897 052
	1-2 yrs	9 939		9 783		10 263		
	FG female	238 478		258 730		192 314		
	FG male	47 875		44 309		43 950		

Appendix 34 : Seasonal protein budgets for the springbok population on the grasslands of Etosha (1973 - 78)

Year	Age-sex class	Population protein requirements (kg DM)						
		Seasonal totals						Yearly total
		Wet, hot season (Jan. to April)		Dry, cold season (May to Aug.)		Dry, hot season (Sept. to Dec.)		
		Class totals	Population total	Class totals	Population total	Class totals	Population total	
1973	0-1 yr	4 539	43 439	5 631	36 161	6 839	23 373	102 973
	1-2 yrs	1 686		1 773		1 865		
	Full grown female	30 957		22 908		8 866		
	FG male	6 257		5 849		5 803		
1974	0-1 yr	5 316	50 881	6 595	42 355	8 010	27 375	120 611
	1-2 yrs	1 978		2 077		2 183		
	FG female	36 257		26 831		10 384		
	FG male	7 330		6 852		6 798		
1975	0-1 yr	7 110	68 044	8 821	56 646	10 713	36 612	161 302
	1-2 yrs	2 639		2 777		2 920		
	FG female	48 494		35 886		13 889		
	FG male	9 801		9 162		9 090		
1976	0-1 yr	8 901	85 201	11 043	70 899	13 413	45 844	201 944
	1-2 yrs	3 305		3 477		3 656		
	FG female	60 721		44 935		17 391		
	FG male	12 274		11 474		11 384		
1977	0-1 yr	17 082	163 503	21 192	136 114	25 739	87 615	387 232
	1-2 yrs	6 344		6 675		7 019		
	FG female	116 525		86 231		33 373		
	FG male	23 552		22 016		21 844		
1978	0-1 yr	17 399	172 533	21 585	138 636	26 217	89 603	400 772
	1-2 yrs	6 462		6 799		7 148		
	FG female	118 686		87 830		33 992		
	FG male	29 986		22 422		22 246		

Appendix 35 : Seasonal protein budgets for the gemsbok population on the grasslands of Etosha (1973 - 78)

Year	Age-sex class	Population protein requirements (kg DM)						
		Seasonal totals						Yearly total
		Wet, hot season (Jan. to April)		Dry, cold season (May to Aug.)		Dry, hot season (Sept. to Dec.)		
		Class totals	Population total	Class totals	Population total	Class totals	Population total	
1973	0-1 yr	1 378	53 796	1 626	32 499	1 819	40 632	126 927
	1-2 yrs	1 923		1 965		2 206		
	Full grown female	45 020		23 949		31 689		
	FG male	5 475		4 959		4 918		
1974	0-1 yr	1 306	50 829	1 541	30 715	1 724	38 397	119 941
	1-2 yrs	1 815		1 855		2 082		
	FG female	42 516		22 616		29 926		
	FG male	5 192		4 703		4 665		
1975	0-1 yr	929	36 474	1 097	22 032	1 227	27 546	86 052
	1-2 yrs	1 305		1 333		1 497		
	FG female	30 526		16 238		21 486		
	FG male	3 714		3 364		3 336		
1976	0-1 yr	569	22 036	671	13 315	751	16 645	51 996
	1-2 yrs	785		802		900		
	FG female	18 436		9 807		12 976		
	FG male	2 246		2 035		2 018		
1977	0-1 yr	777	30 486	917	17 785	1 026	23 024	71 295
	1-2 yrs	1 089		1 113		1 249		
	FG female	25 516		13 573		17 960		
	FG male	3 104		2 182		2 789		
1978	0-1 yr	401	15 688	473	9 478	529	11 850	37 016
	1-2 yrs	559		571		642		
	FG female	13 125		6 982		9 239		
	FG male	1 603		1 452		1 440		

Appendix 36 : Seasonal protein budgets for the red hartebeest population on the grasslands of Etosha (1973 - 78)

Year	Age-sex class	Population protein requirements (kg DM)						
		Seasonal totals						
		Wet, hot season (Jan. to April)		Dry, cold season (May to Aug.)		Dry, hot season (Sept. to Dec.)		
		Class totals	Population total	Class totals	Population total	Class totals	Population total	Yearly total
1973	0-1 yr	100	2 008	117	1 257	132	1 869	5 134
	1-2 yrs	89		93		101		
	Full grown female	1 405		675		1 267		
	FG male	414		372		369		
1974	0-1 yr	131	2 630	154	1 643	173	2 446	6 719
	1-2 yrs	114		118		129		
	FG female	1 847		888		1 665		
	FG male	538		483		479		
1975	0-1 yr	106	2 119	125	1 327	140	1 970	5 416
	1-2 yrs	89		93		101		
	FG female	1 483		713		1 337		
	FG male	441		396		392		
1976	0-1 yr	81	1 625	95	1 014	107	1 511	4 150
	1-2 yrs	65		68		74		
	FG female	1 144		550		1 032		
	FG male	335		301		298		
1977	0-1 yr	56	1 149	66	719	74	1 068	2 936
	1-2 yrs	49		51		55		
	FG female	806		388		727		
	FG male	238		214		212		
1978	0-1 yr	100	2 008	117	1 257	132	1 869	5 134
	1-2 yrs	89		93		101		
	FG female	1 405		675		1 267		
	FG male	414		372		369		

Appendix 37 : Seasonal protein budgets for the ostrich population on the grasslands of Etosha (1973 - 78)

Year	Age-sex class	Population protein requirements (kg DM)						
		Seasonal totals						
		Wet, hot season (Jan. to April)		Dry, cold season (May to Aug.)		Dry, hot season (Sept. to Dec.)		
		Class totals	Population total	Class totals	Population total	Class totals	Population total	Yearly total
1973	0-2 yrs	1 089	5 730	1 173	5 441	1 164	5 414	16 585
	Full grown female	2 317		2 139		2 123		
	FG male	2 324		2 132		2 127		
1974	0-2 yrs	934	4 929	1 006	4 682	997	4 655	14 266
	FG female	1 993		1 840		1 826		
	FG male	2 002		1 836		1 832		
1975	0-2 yrs	905	4 788	975	4 550	967	4 523	13 861
	FG female	1 943		1 795		1 781		
	FG male	1 940		1 780		1 775		
1976	0-2 yrs	884	4 649	952	4 417	945	4 392	13 458
	FG female	1 880		1 736		1 722		
	FG male	1 885		1 729		1 725		
1977	0-2 yrs	1 620	8 520	1 745	8 095	1 730	8 047	24 662
	FG female	3 452		3 187		3 162		
	FG male	3 448		3 163		3 155		
1978	0-2 yrs	955	5 048	1 028	4 794	1 020	4 767	14 609
	FG female	2 043		1 886		1 871		
	FG male	2 050		1 880		1 876		

Appendix 38 : Nutritional status of wildebeest at Etosha as reflected by analyses of blood plasma (1976–78). Age is given as adult (ad.) or, in the case of immatures, to the nearest month or year. The season is given as wet (W) or dry (D). Wet season samples were collected from January to April and dry season samples were collected from May to December.

Age-sex & season	Total protein (g/l)	Albumin (g/l)	Total calcium (mmol/l)	Inorganic phosphorus (mmol/l)	Cholesterol (mmol/l)	Urea (mmol/l)	Total bilirubin (umol/l)	Alkaline phosphatase (Mu/ml)	Glutamic oxalacetic transaminase (mU/l)
2 yr ♂ W	69,8	32,0	2,62	2,13	2,35	8,8	3,0	278	203
Ad. ♀ W	68,0	30,5	2,12	1,81	2,45	8,8	2,0	102	165
Ad. ♂ W	82,8	38,8	2,75	1,75	2,55	8,8	3,0	87	212
2 yr ♀ W	69,5	34,8	2,62	2,98	2,15	8,5	3,0	178	217
1 month ♀ W	44,5	26,5	1,98	2,22	2,00	6,6	2,0	370	112
Ad. ♀ W	70,0	33,5	2,53	1,77	2,00	8,3	3,0	117	193
1 yr ♂ W	56,5	29,3	2,20	2,57	1,65	8,3	3,8	340	201
Ad. ♀ W	68,0	30,7	2,14	1,84	2,35	8,6	2,0	87	168
1 yr ♀ W	45,3	24,2	1,50	2,82	1,35	9,7	3,0	228	>300
Ad. ♂ W	61,0	34,0	2,52	0,63	1,30	7,7	2,0	46	150
Ad. ♂ W	70,5	36,2	2,92	0,77	1,45	6,4	2,0	40	160
Ad. ♂ W	70,0	37,3	2,62	1,01	1,38	4,5	2,5	55	145
2 yr ♀ W	70,4	37,5	2,55	1,30	1,46	8,0	2,0	115	160
Ad. ♂ W	61,6	33,0	2,08	1,18	1,10	7,3	2,2	50	127
Ad. ♂ W	69,8	38,0	2,40	0,90	1,45	8,0	3,0	38	195
2 yr ♀ W	69,0	35,6	2,15	1,95	1,70	8,3	2,5	185	182
Ad. ♂ W	72,0	40,0	2,77	1,17	1,65	9,0	4,0	53	150
Ad. ♂ W	68,0	35,5	2,20	1,48	1,80	8,0	3,0	100	207
Ad. ♀ W	75,0	35,5	2,54	1,75	2,10	8,4	3,0	74	168
Ad. ♂ W	73,0	36,5	2,31	1,40	2,24	5,0	3,0	58	181
Ad. ♀ W	68,0	36,5	2,35	2,13	1,80	12,3	3,0	127	128
Ad. ♂ W	74,5	38,0	2,40	2,15	2,45	7,5	3,0	123	242
Ad. ♂ W	65,0	35,0	2,26	1,98	1,75	8,8	3,0	247	143
Ad. ♂ D	75,0	37,0	2,35	1,93	1,85	4,2	2,5	105	197
Ad. ♂ D	67,2	36,0	2,72	1,43	1,95	3,5	2,0	48	190
Ad. ♂ D	83,0	42,9	2,88	1,77	2,05	7,4	2,0	180	156
Ad. ♂ D	76,0	37,5	2,60	1,55	1,96	5,0	1,9	43	172
Ad. ♂ D	75,5	37,5	2,45	1,50	1,78	4,5	2,0	60	167
Ad. ♂ D	66,3	36,5	1,16	0,82	1,70	5,5	2,0	20	190
Ad. ♂ D	74,8	40,5	2,60	1,40	1,68	5,3	2,8	20	180
Ad. ♂ D	69,0	36,0	2,55	1,30	1,65	3,3	2,0	47	197
Ad. ♂ D	85,0	41,0	3,02	1,68	2,04	4,0	3,0	50	163
Ad. ♀ D	70,8	37,0	2,63	2,03	1,60	4,3	2,0	18	109

Appendix 38 : (continued)

Age-sex & season	Total protein (g/l)	Albumin (g/l)	Total calcium (mmol/l)	Inorganic phosphorus (mmol/l)	Cholesterol (mmol/l)	Urea (mmol/l)	Total bili-rubin (umol/l)	Alkaline phospha-tase (Mu/ml)	Glutamic oxalacetic transaminase (mU/l)
Ad. ♂ D	82,8	44,2	2,50	1,60	1,85	4,7	3,0	23	144
Ad. ♂ D	71,0	35,1	2,45	1,28	2,10	4,8	2,5	40	150
Ad. ♀ D	67,5	46,5	2,35	0,93	2,05	8,7	2,0	70	147
Ad. ♂ D	74,0	41,5	2,20	1,17	1,75	6,7	3,0	38	220
1,5 yr ♀ D	68,0	35,4	2,52	1,13	1,65	5,5	3,0	117	145
1,5 yr ♀ D	74,0	39,2	2,48	1,57	2,35	6,2	2,6	175	114
1,5 yr ♀ D	70,0	37,0	2,65	1,58	2,00	5,7	3,0	178	158
Ad. ♂ D	74,0	43,0	2,12	1,25	1,75	6,2	2,7	61	200
Ad. ♀ D	79,5	40,5	2,59	1,24	2,20	9,8	2,5	47	192
Ad. ♂ D	70,0	39,4	2,43	1,14	1,90	6,3	3,0	34	153
Ad. ♀ D	74,0	39,0	2,41	1,12	1,65	6,3	2,6	55	164
Ad. ♂ D	75,5	35,5	2,37	1,21	3,04	7,7	3,0	164	137
Ad. ♀ D	78,0	40,5	2,26	0,90	2,00	8,0	3,0	67	127
1,5 yr ♂ D	68,0	35,0	2,20	1,33	1,70	6,7	3,0	237	125
1,5 yr ♂ D	64,0	36,0	2,42	1,06	1,70	5,5	3,0	55	127
1,5 yr ♂ D	60,0	30,5	1,94	1,18	1,50	4,4	2,0	115	237
Ad. ♂ D	70,0	39,5	2,17	1,02	1,70	5,2	3,0	27	122
Ad. ♀ D	73,0	39,3	2,12	1,33	1,75	5,3	3,0	37	128
1,5 yr ♂ D	77,0	34,8	2,18	1,28	1,90	5,8	3,0	57	137
1,5 yr ♂ D	72,0	37,0	2,23	1,00	1,85	6,5	3,0	207	157
Ad. ♂ D	69,0	32,0	2,39	0,72	1,70	4,0	3,0	35	142
Ad. ♂ D	66,0	34,5	2,50	0,98	1,45	4,5	3,0	48	122
Ad. ♂ D	72,5	36,5	2,72	1,80	1,75	9,2	3,0	294	162
Ad. ♀ D	78,0	44,0	2,68	2,40	1,60	7,5	3,0	105	168
1,5 yr ♂ D	77,5	45,0	2,82	2,17	1,55	6,0	3,0	102	127
Ad. ♀ D	69,0	40,3	2,48	1,53	1,10	5,7	3,0	27	110
1,5 yr ♂ D	69,0	39,0	2,75	1,84	1,35	4,7	3,0	117	148
Ad. ♂ D	66,0	34,0	2,07	1,05	1,65	7,8	4,0	38	125
Ad. ♂ D	59,5	29,0	2,55	0,82	1,45	5,3	3,0	46	117
Ad. ♂ D	64,0	33,0	2,72	0,73	1,32	6,4	3,0	75	131
Ad. ♀ D	57,5	33,5	2,60	1,07	1,85	5,0	4,5	30	123
Ad. ♀ D	63,0	33,5	2,40	1,15	1,65	4,4	4,0	50	127
2 yr ♀ D	59,0	29,5	2,60	1,15	1,45	5,2	3,0	90	127