

# Nutritional balance between grassland productivity and large herbivore demand in the Etosha National Park

by

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## 1 INTRODUCTION

This investigation formed part of a larger study directed primarily at establishing which environmental factors were responsible for the drastic decline in blue wildebeest *Connochaetes taurinus* numbers in the Etosha National Park in northern South West Africa / Namibia (Berry, 1980). Here we estimate energy and protein requirements in the major large herbivores inhabiting the grasslands of Etosha, taking into account their age-sex ratios and population trends. Thereafter, we balance the energy-protein supply of the grasslands against the seasonal demand for these critical nutrients by the large herbivores. This approach makes it possible to establish whether competition for food existed and if so, which seasons and areas were involved.

The six major herbivore species involved were blue wildebeest, Burchell's zebra *Equus burchelli*, springbok *Antidorcas marsupialis*, gemsbok *Oryx gazella*, red hartebeest *Alcelaphus caama*, and ostrich *Struthio camelus*. All are large in size and were relatively easy to observe from a vehicle, although springbok were often overlooked during aerial censuses. The red hartebeest, by preference a bush and woodland dweller in Etosha, was not uncommon on the plains. Consequently, we have included this species 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.

## 2 METHODS

### 2.1 Aerial counts

Estimates of the numbers of large herbivores were made during aerial censuses (Berry, 1980). We carried out four major censuses by helicopter from 1974 - 78 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.

## ABSTRACT

A first approximation of the total demand of energy and protein by six large herbivore species, namely blue wildebeest, Burchell's zebra, springbok, gemsbok, red hartebeest and ostrich, was balanced against the measured supply of these critical nutrients, 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.

## 2.2 Ground observations

More detailed age-sex classes were established during observations made from a vehicle, over a period of four years (1974 – 78). The herbivores were sexed and divided into various age classes: less than one year old, one to two years old, two to three years old, full grown or adult. To avoid bias in determining the population structure, family units or whole herds were aged and sexed when possible.

## 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 in Etosha, we applied the increments over resting metabolic rate (RMR) which had been established for the various age-sex classes of wildebeest (Berry and Louw, 1982a) 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. We 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. 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, we used a mean fresh egg mass of 1 187g (Sauer and Sauer, 1966) and, based on the mean mass of 10 ostrich egg shells which was found to be 19% of the total egg mass, we 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, we estimated that one egg would contain 1 596 kcal. Furthermore, based on data for domestic animals (Crampton and Harris, 1969), we 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<sup>-1</sup>. Because the rate of successful egg production of ostrich in Etosha is unknown, we 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  $70 W_{\text{kg}}^{0,75}$  kcal.day<sup>-1</sup> (National Research Council, 1966) for all mammalian competitors. For RMR in ostrich we applied Lasiewski and Dawson's (1967) regression equation for non-passerine birds of  $78,3 W_{\text{kg}}^{0,723}$  kcal.day<sup>-1</sup>.

## 2.4 Calculation of protein budgets

Nitrogen requirements for maintenance, growth, gestation and lactation were calculated for the six herbivore species using the equations detailed in Berry and Louw (1982a). In the case of ostrich we estimated nitrogen requirements for egg production. To achieve this we assumed that 125 g protein occurred, on average, in an ostrich egg (Section 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, we multiplied 160 g N by a factor of 1,38 (Crampton and Harris, 1969), thereby obtaining a final estimate of 221 g N.year<sup>-1</sup> per laying hen.

Subsequently, protein budgets were derived for individuals and the populations of all six herbivore species as described in Berry (1980).

# 3 RESULTS

## 3.1 Population estimates and trends

Counts of the large herbivores over an 11-year period (1968 - 1978) were corrected for undercounting bias and are given in Table 1. Since aerial counts are underestimates of the total population of a wild animal species (Melton, 1978a) and furthermore, since 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 not surprising that the results in Table 1 are characterised by great variability.

TABLE 1: Corrected aerial counts of six large herbivore species on the grasslands of Etosha (1968 - 78)

Year*	Method	Species					
		Wildebeest	Burchell's zebra	Springbok	Gemsbok	Red hartebeest	Ostrich
1968	Fixed-wing aircraft (Fwa)	4 073	18 073	3 364	1 902	124	316
1969	Fwa	4 773	22 284	15 351	3 692	95	1 437
1970	Fwa	4 789	14 110	9 892	2 509	88	2 784
1972	Fwa	3 078	16 426	7 025	2 726	110	786
1973	Fwa	2 737	10 244	7 493	1 131	95	603
1973	Fwa	2 528	15 053	10 517	2 764	138	1 802
1973	Helicopter (H)	3 717	13 902	8 367	2 201	128	822
1974	H	3 300	16 002	9 800	2 081	167	707
1976	H	2 360	11 035	16 411	902	103	667
1977	H	3 059	9 414	31 493	1 247	73	1 222
1978	H	2 493	9 166	32 076	642	128	724
	Mean ±SD	3 355 ±876	14 155 ±4 041	13 799 ±9 604	1 982 ±930	114 ±27	1 079 ± 705

\*1968-70 from Ebedes *et al.* (1970)

1972-73 from Joubert *et al.* (1973)

1974-78 from Berry (1980)

### 3.2 Age-sex ratios

In the course of five years (1974 - 78) we aged and sexed the large herbivores from a vehicle and a hide. The majority of these observations were made at water-holes where animals usually approached in file to drink. In total, 24 913 animals were aged visually, of which 9 359 (38%) could be accurately sexed. The results are given in Table 2.

### 3.3 Energetic cost of free existence

Energy budgets for the six major herbivore species were calculated for the individual animals on a daily and yearly basis (Berry, 1980) and are summarised in Table 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 calcula-

ting energy demands for seasons other than 1977/78, our assumption was that the increments over RMR remain the same. The reason for this is that activity budget details (Berry *et al.*, 1982) apply only to 1977/78 and the calculations involved for estimating all the parameters of free existence would be too time-consuming in terms of the small benefit in increased accuracy. Nevertheless, we attempted to set up as many age-sex classes as possible, with their accompanying means in body mass, to calculate  $70 W_{kg}^{0.75}$  and  $78.3 W_{kg}^{0.723}$ . We then applied the number of individuals in each class, rather than taking mean biomass of whole populations. These yearly energy budgets are presented in Table 4. In the case of ostrich we added the energetic cost of egg production and incubation to the increment over RMR, which was 1.9. For example, during the helicopter count of 1973 (Table 1), the ostrich population was estimated to be 822, of which 81.3% (668) were full-grown (Table 2). Furthermore, 49.3% (329) of the full-grown ostrich were hens and 50.7% (339) were cocks (Table 2). Assuming

TABLE 2: Age-sex ratios of six large herbivore species on the grasslands of 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
Wildebeest	11 722 %	7 502 64.0	1 629 13.9	2 591 22.1	6 360 %	1 984 31.2	4 376 68.8
Burchell's zebra	6 680 %	5 417 81.1	545 8.1	718 10.8	559 %	262 46.9	297 53.1
Springbok	4 101 %	2 830 69.0	324 7.9	947 23.1	1 475 %	585 39.7	890 60.3
Gemsbok	936 %	780 83.3	83 8.9	73 7.8	215 %	57 26.5	158 73.5
Red hartebeest	532 %	422 79.3	44 8.3	66 12.4	241 %	112 46.5	129 53.5
Ostrich	942 %	766 81.3	151 16.0	25 2.7	509 %	258 50.7	251 49.3

that 90% (296) of all adult hens laid a complete clutch, then  $296 \times 85\,472 \text{ kJ. year}^{-1}$  (Section 2.3) =  $25\,299\,712 \text{ kJ. year}^{-1}$  would be required for egg production. To calculate the energetic cost of incubation for 1973, we assumed that one hen in three, namely 99 hens, would incubate (Sauer and Sauer, 1966).

TABLE 3: Yearly individual energy budgets for six large herbivore species on the Etosha grasslands (from data in Berry (1980)).

Species	Age-sex class	Energy requirements (megajoules. year <sup>-1</sup> )
Wildebeest	0 - 1 year	5 198
	1 - 3 years	9 526
	Adult female	10 091
Burchell's zebra	Adult male	9 068
	0 - 1 year	9 528
	1 - 2 years	12 833
Springbok	Full-grown female	16 742
	Full-grown male	16 100
	0 - 1 year	2 335
	1 - 2 years	2 878
Gemsbok	Full-grown female	3 063
	Full-grown male	2 751
	0 - 1 year	5 653
	1 - 2 years	9 137
Red hartebeest	Full-grown female	11 664
	Full-grown male	10 169
	0 - 1 year	4 643
	1 - 2 years	7 884
Ostrich*	Full-grown female	9 186
	Full-grown male	8 195
	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 4).

Therefore  $99 \times 20\,490 \text{ kJ. year}^{-1}$  (Section 2.3) =  $2\,028\,510 \text{ kJ. year}^{-1}$  would be required for incubation by hens. Similarly,  $2\,873\,970 \text{ kJ. year}^{-1}$  would be required by incubating cocks.

### 3.4 Nitrogen demand for free existence

Our estimation of the individual, daily nitrogen requirements of the large herbivores is summarised in Table 5.

### 3.5 Protein budgets

Seasonal protein budgets were first calculated for individuals (Table 6) by applying a conversion factor of 6.25 to the daily nitrogen demand (Table 5) to obtain the amount of protein required (ARC, 1965). Thereafter the seasonal protein budgets for populations could be computed for the period 1973 - 78 (Berry 1980) and these are summarised in Table 7. For this purpose the estimated populations in each year (Table 1) were taken in conjunction with the age-sex ratios which had been obtained (Table 2).

## 4 DISCUSSION

### 4.1 Energy supply and demand

The combined supply and demand for energy by the six large herbivore species is set out in Table 8. These data are based on the supply and balance of energy as measured by Berry and Louw (1982b) and the theoretical demand and resultant balance calculated in Section 3.3. From the results obtained in Table 8, it appeared that we 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 our investigation took place during a wet cycle.

We will now discuss the possible errors in our estimates which indicate that we employed a conservative method for calculating energy demand. Firstly, the energetic

TABLE 4: Estimated yearly population energy budgets for six large herbivore species on the Etosha grasslands during the period 1973 - 78 (from data in Berry (1980)).

Species	Year	Total energy requirements (terajoules. year <sup>-1</sup> )
Wildebeest	1973	36.5
	1974	32.4
	1975	29.2
	1976	25.9
	1977	29.2
	1978	24.5
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	1.5
	1976	0.8
	1977	0.6
	1978	1.0
Ostrich	1973	5.5
	1974	5.1
	1975	4.9
	1976	4.8
	1977	8.7
	1978	5.2

TABLE 5: Estimated seasonal individual nitrogen budgets for six large herbivore species on the Etosha grasslands (from data in Berry (1980)).

Species	Age-sex class	Seasonal nitrogen requirements (g.day <sup>-1</sup> )		
		Wet, hot season (Jan. to April)	Dry, cold season (May to Aug.)	Dry, hot season (Sept. to Dec.)
Wildebeest	0-1 yr	10.61	12.10	13.81
	1-3 yrs	14.28	13.92	14.72
	Adult female	32.33	34.32	22.62
Burchell's zebra	Adult male	15.07	13.15	13.15
	0-1 yr	13.38	19.13	22.41
	1-2 yrs	17.86	17.15	18.14
Springbok	Full-grown female	80.56	85.27	63.90
	FG male	19.07	16.53	16.53
	0-1 yr	3.13	3.79	4.64
Gemsbok	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
Red hartebeest	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
Ostrich*	FG male	15.05	13.30	13.30
	0-1 yr	8.33	9.53	10.83
	1-2 yrs	10.84	11.01	12.06
Ostrich*	FG female	34.68	16.26	30.88
	FG male	11.75	10.29	10.29
	0-2 yrs	9.43	9.91	9.91
Ostrich*	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 7).

TABLE 6: Estimated seasonal protein budgets for six large herbivore species on the Etosha grassland (from data in Berry (1980)).

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.)
Wildebeest	0-1 yr	7,958	9,302	10,530
	1-3 yrs	10,712	10,703	11,224
	Adult female	24,246	26,386	17,247
Burchell's zebra	Adult male	11,305	10,107	10,024
	0-1 yr	10,035	14,706	17,088
	1-2 yrs	13,395	13,184	13,832
Springbok	Full-grown female	60,420	65,551	48,724
	FG male	14,303	12,707	12,604
	0-1 yr	2,348	2,913	3,538
Gemsbok	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
Red hartebeest	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
Ostrich*	FG male	11,288	10,224	10,141
	0-1 yr	6,248	7,326	8,258
	1-2 yrs	8,130	8,464	9,196
Ostrich*	FG female	26,010	12,500	23,456
	FG male	8,813	7,910	7,846
	0-2 yrs	7,073	7,618	7,556
Ostrich*	FG female	6,630	6,089	6,039
	FG male	6,855	6,288	6,273

\* The protein cost of egg production was added when calculating the population protein budget (Table 7).

TABLE 7: Estimated yearly population protein budgets for six large herbivore species on the Etosha grasslands during the period 1973 - 78 (from data in Berry (1980)).

Species	Year	Total protein requirements (Metric tons DM)
Wildebeest	1973	174
	1974	154
	1975	139
	1976	123
	1977	139
	1978	117
Burchell's zebra	1973	1 363
	1974	1 570
	1975	1 326
	1976	1 072
	1977	923
Springbok	1973	103
	1974	121
	1975	161
	1976	202
	1977	387
Gemsbok	1973	401
	1974	127
	1975	120
	1976	86
	1977	52
Red hartebeest	1973	71
	1974	37
	1975	5
	1976	7
	1977	5
Ostrich	1973	4
	1974	3
	1975	5
	1976	17
	1977	14
	1978	14

cost of rumination could not be estimated during the study on activity patterns of wildebeest (Berry *et al.*, 1982). Likewise, we only examined the lower critical temperature range encountered by wildebeest (Berry and Louw, 1982a). We also did not consider the energy drain by parasites which, although it may be negligible in the case of wildebeest (Biggs and Anthonissen, 1978, 1979), would almost certainly be a considerable factor in zebra, which carry a much heavier parasite load (Scialdo, 1981). An additional factor which contributed to the underestimated theoretical energy demand was the basis we used for calculating RMR and its various increments (Berry and Louw, 1982a). 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 used for maintenance, activity, growth and reproduction. He estimated that 3 - 20% of the gross energy is lost to the heat of the calorogenic 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 our data are adjusted upward by 18% to compensate for this difference between metabolisable energy and net energy the underestimation of demand (Table 8) is considerably reduced.

Finally, the basic formula which we used to calculate RMR, namely  $70W_{kg}^{0.75}$  (NRC, 1966) is based on domestic ruminants and may be higher in wild ruminants. For example, Rogerson (1966, 1968) has presented data showing that wildebeest may have an RMR of  $104,3 W_{kg}^{0.73}$  which suggested that they would require 20 - 30% more metabolisable energy than domestic cattle. If this estimated increase in energy requirement is applied to our data in Table 8, then the underestimation is reduced further.

Thus, if all these factors which we consider likely to have caused the underestimation in energy demand are taken into account, the difference between our 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), it is clear that errors in estimation of the demand could increase by a factor of 5,2 without exceeding the supply of energy. 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 our estimates have been on the conservative side except for an important assumption that the six herbivore species all eat only grass. This is not the case however and certain species, particularly springbok, utilise significant amounts of browse. In summary then, it would appear as if an adequate supply of energy exists for herbivores in Etosha. This was also borne out by the good nutritional status of the majority of these animals (Berry and Louw, 1982c).

#### 4.2 Protein supply and demand

Protein supply and demand in so far as they affect the large herbivores have been estimated for preferred grazing areas and are presented in Table 9. 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 the rainfall was 75% of the average and was in addition erratically distributed. Under these conditions, the measured supply of crude protein was 18% of that of the previous year when rainfall was 138% above average, that is 577 mm.



TABLE 8: Yearly energy supply and demand by six large herbivore species 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 Theoretical demand Balance: theoretical :actual	882 304 + 578 + 401	+144%
1974	701	Actual supply Theoretical demand Balance: theoretical :actual	2 137 335 + 1 802 + 1 405	+128%
1975	424	Actual supply Theoretical demand Balance: theoretical :actual	No data 296	—
1976	577	Actual supply Theoretical demand Balance: theoretical :actual	2 365 257 + 2 108 + 1 250	+169%
1977	316	Actual supply Theoretical demand Balance: theoretical :actual	803 285 + 518 + 404	+128%
1978	590	Actual supply Theoretical demand Balance: theoretical :actual	1 494 268 + 1 226 + 747	+164%

Mean

SD

Mean underestimation of demand

Mean theoretical balance

Mean measured balance

Mean measured usage

147%

± 19%

58%

+ 1 246TJ

+ 841TJ

695TJ

As in the case of the energy supply and demand there appeared to be no shortage of protein during the wet, hot season. Our 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 (Scialdo, 1981) and the fact that the basic formula of  $70 W_{kg}^{0.75}$  (NRC, 1966) was used in the calculation of endogenous urinary nitrogen (Berry, 1980). As discussed under the energy balance, the large herbivores 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. Nevertheless, the mean measured balance of protein was 2.5 times greater than the mean usage as measured by exclusion plots (Table 9) and errors in our estimate 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) our 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 field observations and is also reflected in the energy demand calculated for 1977 (Table 8). 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 in Etosha, is notably different to the abundant quantities of protein available during the wet season of four months. It is evident that our mean estimate of demand exceeded the mean measured usage by a factor of 1.1 for four of the six years (Table 9). 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, our 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 springbok from the grasslands to adjoining mopane savanna in the dry season. During two years (1976, 1978) very good rains resulted in high grass productivi-

TABLE 9: Seasonal protein supply and demand by six large herbivore species 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 Theoretical demand Balance: theoretical :measured	3 283 793 + 2 490 + 2 288	+109%	1 171 996 + 175 + 617	+28%
1974	701	Measured supply Theoretical demand Balance: theoretical :measured	11 641 1 240 +10 401 + 8 998	+116%	1 738 746 + 992 +1 287	+ 77%
1975	424	Measured supply Theoretical demand Balance: theoretical :measured	No data 615 — —	—	1 900 1 116 + 784 + 900	+87%
1976	577	Measured supply Theoretical demand Balance: theoretical :measured	12 504 1 056 +11 448 + 8 633	+133%	2 143 411 +1 732 +1 154	+ 150%
1977	316	Measured supply Theoretical demand Balance: theoretical :measured	2 215 427 + 1 788 + 1 707	+ 105%	1 284 939 + 345 + 818	+ 42%
1978	590	Measured supply Theoretical demand Balance: theoretical :measured	7 519 1 086 + 6 433 + 4 862	+132%	1 469 385 +1 084 + 751	+144%
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

ty, keeping herbivores on the open plains for most of the year. Consequently, our 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 we wish to stress is that while most of the large herbivores 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 catholicly 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. There-

fore, although we do not consider the protein factor to be a gross problem in 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 in 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 our 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<sup>2</sup> 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 during drought conditions. This would be aggravated by the present fenced boundaries of Etosha which prevent grazing herbivores from migrating to their traditional dry season 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 during certain seasons of the year. This has been discussed by Berry and Louw (1982c).

#### 4.3 Nutrient supply in relation to drinking water

In addition to the foregoing considerations, we 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. 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 water-hole; 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 we 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, we 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 food-water dependence, competitors of wildebeest in 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, 1972; Hillman and

Hillman, 1977). Management plans in Etosha should take into account the susceptibility of wildebeest to drought conditions when the food-water link becomes critical.

#### 5 SUMMARY

Aerial censuses were used to estimate the total populations of the six major herbivore species, namely wildebeest, 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 herbivores 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.

In the case of ungulates, 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 from 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.

A feature of the theoretical estimate of energy demand for the grazing herbivores 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  $70 W_{kg}^{0.75}$  used to calculate RMR in the free-ranging herbivores may have contributed to the underestimation of energy demand. Consequently, energy was not considered to be a limiting factor for the grazing herbivores during the period 1973-78.

The strong seasonal influence of rainfall on protein levels in the grasslands of Etosha resulted in an abundance of this nutrient for the large herbivores 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. 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, especially in wildebeest. 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 pure grazers such as wildebeest. The susceptibility of wildebeest to drought was further underlined by their daily water requirements 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 food-water link were to become critical during drought conditions.

The overall finding of this investigation was that the large herbivore species inhabiting the Etosha grasslands were not nutritionally stressed during the period 1973–78, 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 these herbivores, especially wildebeest, is however likely to exist during a prolonged drought.

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## 7 REFERENCES

- AGRICULTURAL RESEARCH COUNCIL  
1965: *The Nutrient Requirements of Farm Livestock. 2. Ruminants*. Agricultural Research Council, London.
- BERRY, H.H.  
1980: Behavioural and eco-physiological studies on blue wildebeest (*Connochaetes taurinus*) at the Etosha National Park. Unpubl. Ph.D. thesis, University of Cape Town.
- BERRY, H.H. and LOUW, G.N.  
1982a: First approximation of the energy and protein budgets in free-ranging wildebeest (*Connochaetes taurinus*) in the Etosha National Park. *Madoqua* 13 (1): 71-88.  
1982b: Nutritional measurements in a population of free-ranging wildebeest in the Etosha National Park. *Madoqua* 13 (2): 101-125.  
1982c: Seasonal nutritive status of wildebeest in the Etosha National Park. *Madoqua* 13 (2): 127-139.
- BERRY, H.H., SIEGFRIED, W.R. and CROWE, T.M.  
1982: Activity patterns in a population of free-ranging wildebeest *Connochaetes taurinus* at Etosha National Park. *Z. Tiersychol.* 59: 229–246.
- BIGGS, H.C. and ANTHONISSEN, M.  
1978-79: Parasitological aspect of blue wildebeest survey: Etosha National Park. Unpubl. reports. Veterinary Regional Laboratory, Windhoek.
- CHILD, G.  
1972: Observations on a wildebeest die-off in Botswana. *Arnoldia* 5 (31): 1-13.
- CRAMPTON, E.W. and HARRIS, L.E.  
1969: *Applied Animal Nutrition*. 2nd edition, Freeman, San Francisco.
- DRODZ, A.  
1975: Feeding and Nutrition. In *Methods for Ecological Bioenergetics*, eds. W. Grodzinski, R.Z. Klekowski and A. Duncan. pp. 325-333. IBP Handbook No. 24. Blackwell Scientific Publications, Oxford.
- DURNIN, J.V.G.A. and PASSMORE, R.  
1967: *Energy, Work and Leisure*. Heinemann, London.
- EBEDES, H., MARITZ, N. and DE JAGER, M.  
1970: Interim report on aerial counts of wildlife in Etosha National Park. Dept. report, Division of Nature Conservation and Tourism, SWA Administration.
- HILLMAN, J.C. and HILLMAN, A.K.K.  
1977: Mortality of wildlife in Nairobi National Park, during the drought of 1973-1974. *E. Afr. Wildl. J.* 15: 1-18.
- JANIS, C.  
1976: The evolutionary strategy of the Equidae and the origins of rumen and cecal digestion. *Evolution* 30: 757-774.
- JOUBERT, E., DU PREEZ, J.S. and GROBLER, H.J.W.  
1973: Lugsensus van die wild in die Nasionale Etosha-wildtuin gedurende September 1973 met behulp van 'n helikopter. Dept. report. Division of Nature Conservation and Tourism, SWA Administration.
- LASIEWSKI, R.C. and DAWSON, W.R.  
1967: A re-examination of the relation between standard metabolic rate and body weight in birds. *Condor* 69: 13-23.
- MAYNARD, L.A. and LOOSLI, J.K.L.  
1962: *Animal Nutrition*. 5th edition. McGraw Hill, New York.
- MELTON, D.A.  
1978a: Undercounting bias of helicopter censuses in Umfolozi Game Reserve. *Lammergeyer* 26: 1-6.  
1978b: The validity of helicopter counts as indices of trend. *Lammergeyer* 26: 38-43.
- MOEN, A.N.  
1973: *Wildlife Ecology*. Freeman, San Francisco.
- NATIONAL RESEARCH COUNCIL  
1966: *Biological energy interrelationship and glossary of energy terms*. Publication No. 1411, National Academy of Sciences. Washington, D.C.
- ROGERSON, A.  
1966: The utilisation of metabolisable energy by a wildebeest. *E. Afr. Wildl. J.* 4: 149  
1968: Energy utilisation by the Eland and Wildebeest. In *Comparative Nutrition of Wild Animals*, ed. M.A. Crawford, pp. 153-161. *Symp. zool. Soc. London* 21. Academic Press, London.
- SAUER, E.G.F. and SAUER, E.M.  
1966: The behaviour and ecology of the South African ostrich. *Living Bird* 5: 45-75.
- SCIALDO, R.C.  
1981: Biology and meaning of zebra parasitism. Report delivered at the Annual Meeting of Professional Officers, Nature Conservation Branch, Windhoek. October 1981.
- SIEGFRIED, W.R. and FROST, P.G.H.  
1974: Egg temperature and incubation behaviour of the ostrich. *Madoqua* Ser. 1 (8): 63-66.
- VAN DER SPUY, J.S.  
1960: Annual report of the biologist. Division of Nature Conservation and Tourism, SWA Administration.
- WESTERN, D.  
1975: Water availability and its influence on the structure and dynamics of a savannah large mammal community. *E. Afr. Wildl. J.* 13: 265-286.