

Seasonal nutritive status of wildebeest in the Etosha National Park

by

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1 INTRODUCTION

Our investigation was designed to assess the nutritional status of a free-ranging wildebeest *Connochaetes taurinus* population on a seasonal basis. It was part of a study undertaken to establish the reasons for the sharp decline in wildebeest numbers in the Etosha National Park in northern South West Africa/Namibia (Berry, 1980). Consequently, we attempted an objective assessment of the condition of individuals from the Etosha population, using internal examinations to predict their chance of survival. Because detailed internal examination is time-consuming we also subjectively assessed the external physical condition of a large and representative sample of the population at critical seasons.

2 METHODS

2.1 Visual ratings

Since the external physical appearance of an ungulate is a good indicator of its nutritional status (Riney, 1960), we used five mutually exclusive categories whereby the nutritive level of wildebeest could be subjectively measured. The physical appearance of a wildebeest was judged by the degree to which the skeletal details of its body were visible (Fig. 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 showing slightly |
| 3 (fair) | = | hindquarters angular in appearance and ribs well defined |
| 2 (poor) | = | pelvic bones prominent and ribs protruding |
| 1 (very poor) | = | skeletal details clearly visible and rump concave; general appearance, posture and coat condition deteriorated. |

In total we carried out visual ratings on 67 marked wildebeest, which were resighted at regular intervals, and on the population (n=3 898) during the period 1976 - 79.

ABSTRACT

The nutritive status of wildebeest was assessed using visual condition ratings, kidney fat, bone marrow and blood plasma as indicators of nutritional stress. Visual physical ratings showed that 78% of wildebeest were in good to excellent condition. This was confirmed by the kidney fat index. Thirteen out of 20 wildebeest had a bone marrow fat level above 80%. Nine blood parameters were measured, confirming that nutritive levels were normal, except for inorganic phosphorus which was marginally deficient. Similarly, liver analyses showed low phosphorus levels and suggested that copper and cobalt may also have been marginally deficient. Nevertheless, nutritive levels were sufficiently high to discount nutrition as being limiting to the population.

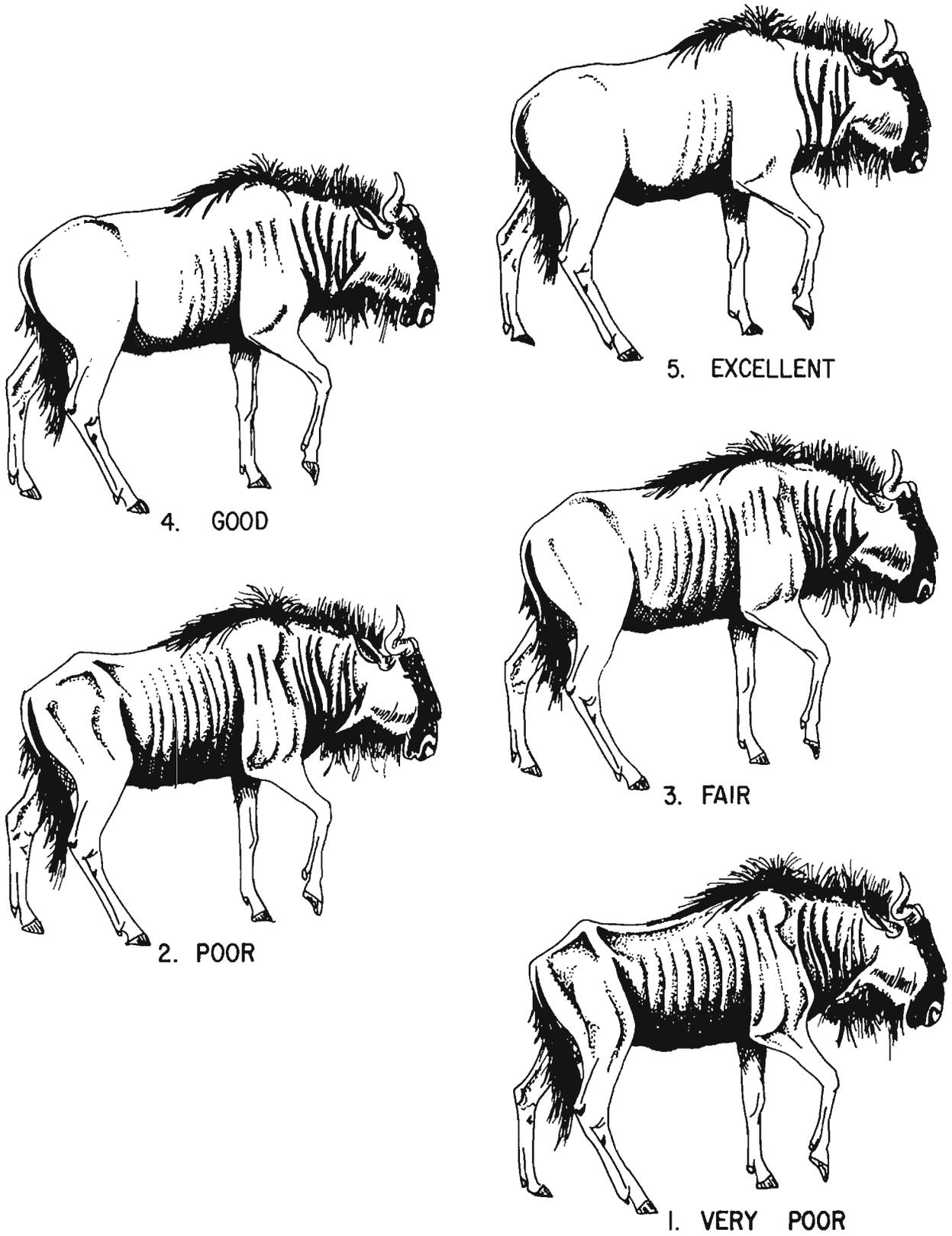


FIGURE 1: Diagrammatic presentation of the five categories used to estimate the nutritional status of wildebeest in Etosha (1976 – 79).

2.2 Kidney fat

Kidneys from 19 shot wildebeest, 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 Smith (1970) and expressed as:

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

2.3 Bone marrow fat

Since 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), it is a critical measurement of condition when stress becomes extreme. We collected between five and 20 g of fresh bone marrow from each of 20 wildebeest which had been shot or killed by lions. Marrow fat from the tibia or femur 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. Subsequently, the percentage dry fat residue was calculated.

2.4 Blood analyses

To investigate whether a relationship existed between certain blood parameters and the nutritive level 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 separation in a portable, clinical centrifuge set at 7 000 rpm and immediately cooled to -20°C using carbon dioxide. Analyses were done by auto-analytic methods (Model SMA 12/60) and the results recorded on charts (No. 940-0859-02A).

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 $\mu\text{mol/l}$.

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.

3 RESULTS AND DISCUSSION

3.1 Visual physical condition

To simplify the presentation of data, we 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 1 to 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, while the majority (62%) were in good condition. The category of excellent condition was awarded to 16% of all animals observed.

We 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

TABLE 1: Visual physical condition of adult wildebeest bulls in 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	60
	Dry, cold	0	0	34	53	13	
	Dry, hot	0	4	46	48	2	
1978	Wet, hot	0	0	18	60	22	112
	Dry, cold	0	0	19	56	25	
	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 2: Visual physical condition of adult wildebeest cows in 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	60
	Dry, cold	0	0	18	37	45	
1978	Dry, hot	0	2	21	51	26	112
	Wet, hot	0	1	41	53	5	
	Dry, cold	2	1	13	48	36	
1979	Dry, hot	0	8	8	73	11	110
	Wet, hot	0	10	17	40	33	
Mean		<1	2	22	52	23	111

*n = 1 234 observations

TABLE 3: Visual physical condition of immature wildebeest aged one to two years in 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	
1978	Dry, hot	0	0	21	74	5	112
	Wet, hot	0	0	7	92	1	
	Dry, cold	0	0	15	74	11	
1979	Dry, hot	0	0	26	70	4	110
	Wet, hot	0	0	19	77	4	
Mean		0	0	18	73	9	111

*n = 540 observations

TABLE 4: Visual physical condition of wildebeest calves, less than one year old, in 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	1	4	91	4	161
	Dry, hot	0	0	32	49	19	
1977	Wet, hot	1	1	9	85	4	60
	Dry, cold	<1	<1	4	91	4	
1978	Dry, hot	0	0	33	51	16	112
	Wet, hot	<1	<1	9	87	3	
	Dry, cold	0	0	31	46	23	
1979	Dry, hot	0	0	25	58	17	110
	Wet, hot	0	<1	17	77	6	
Mean		<1	<1	18	71	10	111

*n = 1 021 observations

than 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, 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 ex-

cellent 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 mean annual rainfall during this period was 476 mm (average for area 419 mm), except during 1977 when it was 60 % of the 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 grass productivity.

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 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

(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 our 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 5 of this investigation).

From the results of our 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.

3.3 Relationship of bone marrow fat to nutritional stress

Applying the t statistic for two means, we found no significant difference in fat content of the marrow during

TABLE 5: Kidney fat index of wildebeest in 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	

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

TABLE 6: Bone marrow fat of wildebeest in Etosha on a seasonal basis (1978).

Season	Age-sex and social class	Visual ratings		Percentage bone marrow fat
		Physical condition	Marrow colour*	
Wet	One-month old cow	Excellent	White, opaque	92,5
	Two-month old bull	Very poor	Pink, gelatinous	3,0**
	One-year old cow	Fair	White, opaque	94,5
	One-year old bull	Fair	White, opaque	95,7
	Two-year old cow	Good	White, opaque	94,5
	Two-year old bull	Good	White, opaque	88,0
	Adult cow, not lactating	Excellent	White, fatty	97,0
	Adult cow, lactating	Fair	Pink, opaque	69,3
	Adult bull, bachelor	Excellent	White, fatty	95,8
	Adult bull, territorial	Excellent	White, fatty	99,1
	Mean	—	—	91,8
SD	—	—	±9,0	
Dry	Three-month old cow	Very poor	Pink, gelatinous	2,3**
	Eight-month old cow	Excellent	White, opaque	96,7
	21-month old cow	Excellent	White, opaque	60,1
	21-month old bull	Good	White, opaque	98,5
	Adult cow, pregnant	Poor	Pink, opaque	78,8
	Adult cow, pregnant	Good	White, fatty	91,5
	Adult cow, pregnant	Excellent	White, fatty	98,3
	Adult bull, bachelor	Good	White, fatty	85,5
	Adult bull, territorial	Fair	Pink, opaque	39,4
	Adult bull, territorial	Fair	Pink, opaque	39,5
	Mean	—	—	76,5
SD	—	—	±24,2	

* According to Sinclair and Duncan (1972)

**Values not included in calculation of the means; explanation given in text

the wet and dry seasons at $P > 0,05$ (Table 6). 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 in Etosha were not sufficiently severe to cause mobilisation of marrow fat reserves.

Certain marrow samples which had a marrow content of less than 80% (Table 6) deserve closer scrutiny. Two samples (69,3% and 78,8% 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 5) which is consistent with the findings of Sinclair and Duncan (1972), namely that kidney fat is mobilised before bone marrow fat.

In the case of two adult, territorial bulls the marrow fat contents were very similar at 39,4% and 39,5%. 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 (2,3% and 3,0%) 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 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.

3.4 Blood status

Blood analyses of Etosha's wildebeest are given in Table 7.

3.4.1 Plasma proteins

The plasma samples from wildebeest ($n = 66$) had a total protein mean value of 69,65 g/l \pm 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 the wildebeest cows may have been induced by growth in young animals or by preg-

nancy, which may lower the circulating levels of proteins, particularly albumin (Doxey, 1971). However, the albumin level of bulls ($\bar{x} = 36,81$ g/l) and cows ($\bar{x} = 35,73$ g/l) in 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 ($\bar{x} = 71,12$ g/l) than immatures ($n = 19$) ($\bar{x} = 64,44$ g/l) at $P < 0,01$. Also, the albumin in

adult plasma ($\bar{x} = 37,20$ g/l) was at a higher level than that of immatures ($\bar{x} = 34,49$ 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 ($\bar{x} = 71,04$ g/l)

TABLE 7: Nutritional status of wildebeest in 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	2,32	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
\pm 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^*	-2,12	-3,13	-0,85	-1,04	-0,83	3,19	0,69
p^{**}	<0,05	<0,01	>0,10	>0,10	>0,01	<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^*	1,63	0,99	0,62	0,41	0,60	-2,13	-0,70
p^{**}	>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^*	3,01	2,41	0,74	0,73	0,80	-3,03	0,76
p^{**}	<0,01	<0,02	>0,10	>0,10	>0,10	<0,01	>0,10

TABLE 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
\pm 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

than during the wet season ($\bar{x} = 67,05$). This was contrary to the levels of crude protein existing in the forage at these seasons (Berry and Louw, 1982) but was in accordance with our findings at that time, namely that faecal crude protein was significantly higher during the dry season than during the wet season. We ascribed this to factors such as food selection and the ability of ruminants to synthesise their protein from non-protein nitrogenous compounds via microbial action in the rumen.

The albumin fraction of the plasma protein of Etosha's wildebeest ($\bar{x} = 36,42$ 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 had 52.29% albumin in their TPP, which was at the midpoint of this range.

3.4.2 Total and ionised calcium

The mean calcium level in all wildebeest plasma samples was $2,41 \text{ mmol/l} \pm 0,31$ (range 1,16 - 3,02). This was within the range of the means reported for bovines, namely $2,32 \text{ mmol/l}$ (Doxey, 1971) and $2,77 \text{ mmol/l}$ (Belonje, 1978). Alaskan moose, considered to be in good to excellent condition, had a level of $2,60 \text{ mmol/l}$ 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, we 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). Coles 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, we used the formula:

$$\text{Ca}^{++} \text{ mmol/l} = \frac{720 \text{ Ca}_{\text{total}} - \text{TPP}}{12 \text{ TPP} + 720}$$

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

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, we computed the regression equation by the method of least squares. No linear relationship between these two parameters could be found on a seasonal, sexual or age basis.

3.4.3 Inorganic phosphorus

Mean inorganic phosphorus present in wildebeest plasma was $1,47 \text{ mmol/l} \pm 0,51$ (range 0,72 - 2,82). Normal bovine levels are $2,87 \text{ mmol/l}$ for calves and $1,78 \text{ mmol/l}$ 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 $1,62 \text{ mmol/l}$, whilst those in a habitat with sufficient phosphorus in the soil had a level of $3,66 \text{ mmol/l}$ (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 in 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 rain-water pools, river water, boreholes or artesian wells and very low levels in fountains from which wildebeest prefer to drink ($0,001 \text{ mmol/l}$; Berry and Louw, 1982).

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, although we 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), we 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. 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 (Berry *et al.*, 1982). 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 coincided with the findings of this study.

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 \pm 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 \pm 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). We will discuss this stress factor in our conclusions. Since it is unlikely that anaemia or organ dysfunction were involved in Etosha wildebeest (Basson, 1979, pers. comm.), we examined the dietary fat levels which were obtained when analysing the grass (Berry and Louw, 1982).

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. In addition, no statistical differences in the circulating level of cholesterol were found to occur on either a seasonal, 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.

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 \pm 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). Doxey 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 ($\bar{x} = 8,06$ mmol/l) than during the dry season ($\bar{x} = 5,78$ 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 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 during the wet season in Etosha, possibly exceeding the levels which could be utilised by wildebeest (Berry and Louw, 1982). 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 (Berry and Louw, 1982) 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 (Berry and Louw, 1982) give additional support to this argument.

3.4.6 Bile pigments

The mean value of total bilirubin in wildebeest plasma was 2,78 mmol/l \pm 0,56 (range 1,9– 4,5). 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, we 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.

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 $99.24 \text{ Mu/ml} \pm 18,0$ (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 as already discussed. 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).

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 $161,26 \text{ mU/ml} \pm 37,05$ (range 109 — > 300). The literature gives a wide range of normal GOT values for domestic cattle. For instance, Coles (1967) reports $438 \pm 57 \text{ mU/ml}$ 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 ($P > 0,10$). We therefore 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.

3.4.9 Iron

A mean iron level of $24,69 \text{ umol/l} \pm 6,88$ (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). In 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 ($\bar{x} = 20,65 \text{ umol/l}$) 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.

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.

3.5 Liver status

The results of wildebeest liver analyses are given in Table 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. 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. 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.

TABLE 8: The nutritional status of wildebeest in Etosha as reflected by liver analyses (1978 – 79).

Measurement	Liver constituent (umol/l)								
	Calcium	Phosphorus	Magnesium	Copper	Manganese	Zinc	Iron	Cobalt	Selenium
Wildebeest*									
Maximum	96	7 174	264	136	11,0	952	1 300	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**									
Maximum	1 529	15 200	417	589	3,0	479	1 521	–	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

*Present study; **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)

3.5.1 Macro-elements

In contrast to blood calcium levels, liver 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 our earlier supposition that inorganic phosphorus may be marginally deficient in the forage and water available to wildebeest in 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 8).

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.

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 carcasses in Etosha for anthrax in the blood (Ebedes, 1976) 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 nutritive status was not detrimentally influenced by inadequacy of the trace element nutrition.

4 SUMMARY

Visual physical rating of 3 898 wildebeest showed that 78% 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 during the three-year visual sampling period did the population appear to be nutritionally stressed. The kidney fat index supported the visual condition ratings, confirming that Etosha's wildebeest were in a healthy state of nutrition. Similarly, 13 of 20 wildebeest sampled had a marrow fat level of more than 80%. Lowered levels of marrow fat were associated with rutting, pregnancy and lactation and, in the case of calves, separation from the mother. Bone marrow fat appeared to be the most sensitive indicator for assessing whether severe nutritional stress was present.

The analysis of nine blood parameters confirmed that Etosha's wildebeest were at a normal level of nutrition in most nutrients except inorganic phosphorus. There appeared to be a seasonally induced chronic shortage of this critical element in circulation. The level of the wet season, although significantly higher than that of the dry season, 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. 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. Gross haemocytological investigation did not reveal any cellular abnormalities in the blood, which supported the findings that the trace element supply was adequate. The overall findings of this investigation indicated that the nutritive level of wildebeest in Etosha was sufficiently high to discount nutrition as being a limiting factor for the population.

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