Population statistics and carrying capacity of large ungulates in the Whovi Wild Area, Rhodes Matopos National Park, Zimbabwe Rhodesia

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Population data for introduced large ungulates, are presented to demonstrate population growth in terms of numbers and biomass in the Whovi Wild Area of the Rhodes Matopos National Park, Zimbabwe Rhodesia. Peak calving in relation to food requirements of different species is discussed. Standing crop of large ungulates was calculated and compared with carrying capacity as predicted by Coe *et al.* (1976).
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Bevolkingsdata vir ingevoerde hoefdiere word voorgestel om die bevolkingsgroei in terme van getalle en biomassa in die Whovi Wildgebied van die Rhodes Matopos Nasionale Park, Zimbabwe Rhodesië. Spitskalftydperk in verhouding tot voedselvereistes van verskillende spesies word bespreek. Massa van groot hoefdiere is bereken en vergelyk met drakapasiteit soos deur Coe *et al.* (1976) voorspel.
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A variety of large ungulate species have since 1960 been released into the western portion of the Rhodes Matopos National Park to increase the spectrum of wild life. The initial introductions into the 'game park', now called the Whovi Wild Area, were reported by Wilson (1969). Since then more animals have been introduced to the area which now contains populations of 17 species of large ungulates. White rhino *Ceratotherium simum*, zebra *Equus burchelli*, hippo *Hippopotamus amphibius*, warthog *Phacochoerus aethiopicus*, giraffe *Giraffa camelopardalis*, buffalo *Syncerus caffer*, eland *Taurotragus oryx*, roan *Hippotragus enquinus*, sable *H. niger*, waterbuck *Kobus ellipsiprymnus*, tsessebe *Damaliscus lunatus*, wildebeest *Connochaetes taurinus* and impala *Aepyceros melampus* have been introduced while non-introduced species include bushpig *Potamochoerus porcus*, kudu *Tragelaphus strepsiceros*, bushbuck *T. scriptus* and reedbuck *Redunca arundinum*.

The topography and vegetation types of the Park have been discussed in Grobler and Wilson (1972), Grobler (1974) and Smith (1977) while Grobler and Van der Meulen (1975) reviewed the history of the area.

The size of the Whovi Wild Area (10 597 ha) and the introduction of small numbers of large ungulates provided an unique opportunity to study aspects of their population ecology.

Methods

The topography of the area is such that most of the large ungulates could be monitored by routine patrols supplemented by an intensive annual ground count on foot and during October or November when visibility was good by vehicle. Population structure and distribution was recorded on a continuous basis to gain knowledge on calving success and population trends. Any animal found dead was examined for cause of death and the skull collected to prevent duplication of recording. It is recognized that young animals are under-represented by found carcasses (see Spinage 1972), but with the older animals in the Park a high proportion was recovered. In July 1973 for example, 11 roan were introduced into the area and eight of these died over the following two months. All of the eight carcasses were recovered, some in remote areas several weeks after death.

The White rhino are all known individually and accurate records are kept of these. Photographs of horn

Table 6 Blue wildebeest (*Connochaetes taurinus*): General statistics for samples compared

Sample No.	No. in sample	Component 0°	Component 90°	Resultant (length)	R/N	Angle of R (degrees)	Confidence intervals for angle of modal vector 95% (degrees)		99% (degrees)	
1	101	54,840	19,392	58,168	0,576	19,474	7,3	31,6	4,3	34,6
2	100	57,597	11,746	58,783	0,588	11,526	−0,4	23,4	−3,3	26,4
3	100	14,255	18,598	23,433	0,234	52,530	16,3	88,8	1,5	103,6
4	100	51,420	17,567	54,338	0,543	18,862	5,8	31,9	2,6	35,1
5	101	38,983	37,917	54,382	0,538	44,206	31,1	57,3	17,9	60,5
6	101	33,173	24,102	41,004	0,406	36,001	17,4	54,6	11,9	60,1
7	99	37,524	3,443	37,682	0,381	5,243	−14,7	25,2	−20,7	31,2
8	100	46,262	−40,026	61,174	0,612	319,134	307,8	330,5	305,0	333,3
9	100	36,946	−48,791	61,201	0,612	307,134	295,8	318,5	293,0	321,2
10	100	8,077	−25,316	26,574	0,266	287,694	256,3	319,1	244,4	331,0
11	100	27,122	33,793	43,331	0,433	51,249	33,7	68,8	28,5	74,0
12	99	−32,253	5,135	32,659	0,330	170,955	146,0	195,9	137,2	204,7

Table 7 Blue wildebeest (*Connochaetes taurinus*): Multi-sample tests

1. Test to determine whether the dispersion parameters are the same, i.e. $H_0 : \kappa_1 = \kappa_2 = \ldots = \kappa_s$
Observed value Z = 34,080

Critical value	Significance level	Conclusion
17,275	0,100	Reject H_0
19,675	0,050	Reject H_0
21,920	0,025	Reject H_0
24,725	0,010	Reject H_0
26,757	0,005	Reject H_0

Rejection of the null hypothesis indicates that the preferred direction in which the animals face changes with time.

2. The test to compare modal vectors was not performed since the null hypothesis ($H_0 : \kappa_1 = \kappa_2 \ldots \kappa_s$) was rejected.

Table 8 Difference between the angle of the sun and preferred angle of orientation of Blue wildebeest (*Connochaetes taurinus*)

Sample No.	Sun angle (degrees)	Resultant angle (degrees)	Difference between sun & resultant angles (degrees)
1	70	19,5	50,5
2	45	11,5	43,5
3	35	52,5	17,5
4	20	18,9	1,1
5	10	44,2	34,2
6	360	36,0	36,0
7	350	5,2	15,2
8	337	319,1	17,9
9	315	307,1	7,9
10	305	287,7	17,3
11	295	51,2	116,2
12	275	171,0	104,0

Table 9 Breeding seasons of the White-fronted sandplover (*Charadrius marginatus*): General statistics for samples compared

Sample No.	No. in sample	Component 0°	Component 90°	Resultant (length)	R/N	Angle of R (degrees)	Confidence intervals for angle of modal vector 95% (degrees)		99% (degrees)	
1	23	−9,203	−14,107	16,843	0,732	236,880	218,1	255,7	213,1	260,7
2	21	−16,086	−5,449	16,984	0,809	198,715	181,5	215,9	175,9	221,6

Table 10 Breeding seasons of the White-fronted sandplover (*Charadrius marginatus*): Two-sample tests

1. Test to determine whether the dispersion parameters are the same $H_0 : \kappa_1 = \kappa_2$
Observed value $U = ((N_1 - R_1)(N_2 - 1))/(N_2 - R_2)(N_1 - 1)) =$ 1,394

Critical value	Significance level	Conclusion
2,434	0,050	Accept H_0
2,780	0,025	Accept H_0
3,266	0,010	Accept H_0
3,658	0,005	Accept H_0
4,665	0,001	Accept H_0

2. Test to determine whether the modal vectors are the same (assuming $\kappa_1 = \kappa_2$)
Observed value $Z = (R_1 + R_2)/N = 0{,}769$

Critical value	Significance level	Conclusion
0,744	0,100	Reject H_0
0,751	0,050	Reject H_0
0,758	0,025	Reject H_0
0,789	0,001	Accept H_0

profiles and ear markings are continually updated to ensure accurate identification at all times. The giraffe are also known individually from photographs showing the coat pattern and a programme is presently in progress to identify and document all the zebra using the method of Peterson (1972).

The estimates of the populations of other species were based on annual counts augmented with records from routine monitoring patrols. Biomass figures for each species were calculated using unit mass figures given by Coe, Cumming and Phillipson (1976). Data presented for Matopos cover the period 1960 to the end of 1977, the only exception being some of the rhino births, zebra births and one hippopotamus birth.

Results

The numbers and biomass of the 17 large ungulates species which occur in the Whovi Wild Area are given in Table 1. The counts are considered to be accurate for rhino, zebra, hippopotamus, giraffe, buffalo, eland, roan, tsessebe, wildebeest and impala, all of which have been introduced sinced 1960. The counts of the other species are less accurate due to a combination of their size, habits or the fact that natural populations of unknown number occurred in the area prior to the introduction.

Table 1 Estimated population and biomass of 17 large ungulate species in the Whovi Wild Area of the Rhodes Matopos National Park

Species	Population	Unit mass (kg)*	Biomass per species (kg)
White Rhino	26	1 500	39 000
Zebra	24	200	4 800
Hippopotamus	4	1 000	4 000
Warthog	150	45	6 750
Bushpig	140	54	7 560
Giraffe	9	750	6 750
Buffalo	130	450	58 500
Eland	100	340	34 000
Kudu	10	136	1 360
Bushbuck	20	30	600
Roan	3	220	660
Sable	150	185	27 750
Waterbuck	20	160	3 200
Reedbuck	150	40	6 000
Tsessebe	15	91	1 365
Wildebeest	145	123	17 835
Impala	275	40	11 000
Total	1 371	–	231 130

*From Coe *et al.* 1976.

The increase in numbers of White rhino, zebra, giraffe, buffalo, eland, wildebeest and impala between 1960 and 1977 is shown in Table 2. The data from this table for the five most successful of these introduced species were used to illustrate growth in number and biomass (Fig. 1A and 1B). The two graphs show that the growth of the populations of these species tended to follow a sigmoid curve and with the exception of rhino had reached a peak in 1976. The biomass graph magnifies the plots for population growth of very large animals while reducing them for smaller more numerous animals such as impala. It also illustrates the importance of rhino which is second only to buffalo in terms of biomass though in terms of numbers it would appear to be the least important species. The decrease in number of wildebeest in 1974 and rhino in 1975 was a result of capture and translocation exercises. The sudden check in the growth rate of the impala population between 1976 and 1977 was due to the translocation of 32 animals.

The number of births for 10 species recorded on a monthly basis is given in Table 3. The numbers of births recorded for rhino and giraffe represent the total number of births from 1960 to 1978. Those of the other species were recorded from 1974 to 1978 with the exception of warthog which were recorded from 1976 to 1978 and do not represent the total numbers of births for those periods. They do, however, give an accurate indication of the calving season for those periods. The calving seasons are indicated graphically in Fig. 2 where the number of births per month are shown as a percentage of the total number of recorded births.

Discussion

Breeding

Calving has been shown to coincide with optimal food requirements for the adult female and her calf for several African ungulates (Talbot & Talbot 1963; Von Richter 1971; Skinner, Van Zyl & Oates 1974; Hall-Martin, Skinner & Van Dyk 1975). Sinclair (1974) showed buffalo births correlated with months of high rainfall and Grimsdell (1973) found a bimodal peak of births coinciding with the middle of two rainy seasons in one population and the early part of the rains in another.

The combined breeding data in the Matopos study area showed that the two large ungulate species, giraffe and white rhino calved throughout the year. In the study area the former is almost exclusively a high level browser and the latter almost entirely a low level grazer. The level at which various herbivores feed is suggested as a critical

Table 2 Annual change in numbers of seven ungulate species from 1960 – 1977 in the Whovi Wild Area of the Rhodes Matopos National Park

Species	1960	1961	1962	1963	1964	1965	1966	Year 1967	1968	1969	1970	1971	1972	1973	1974	1975	1976	1977
White Rhino	–	–	4	4	4	4	11	13	15	18	19	20	21	24	26	23	24	26
Zebra	5	4	4	4	4	6	5	5	8	8	8	9	9	11	11	17	22	24
Giraffe	6	2	4	2	2	2	2	3	3	3	4	4	3	5	5	7	8	8
Buffalo	–	–	10	10	14	13	20	26	34	–	–	60	66	75	100	120	130	130
Eland	8	9	10	10	13	15	19	21	–	–	45	45	–	65	85	90	100	100
Wildebeest	12	13	18	32	36	46	57	75	–	–	115	125	–	145	115	140	145	145
Impala	4	5	13	20	25	34	51	76	–	–	125	150	–	200	225	250	175	275

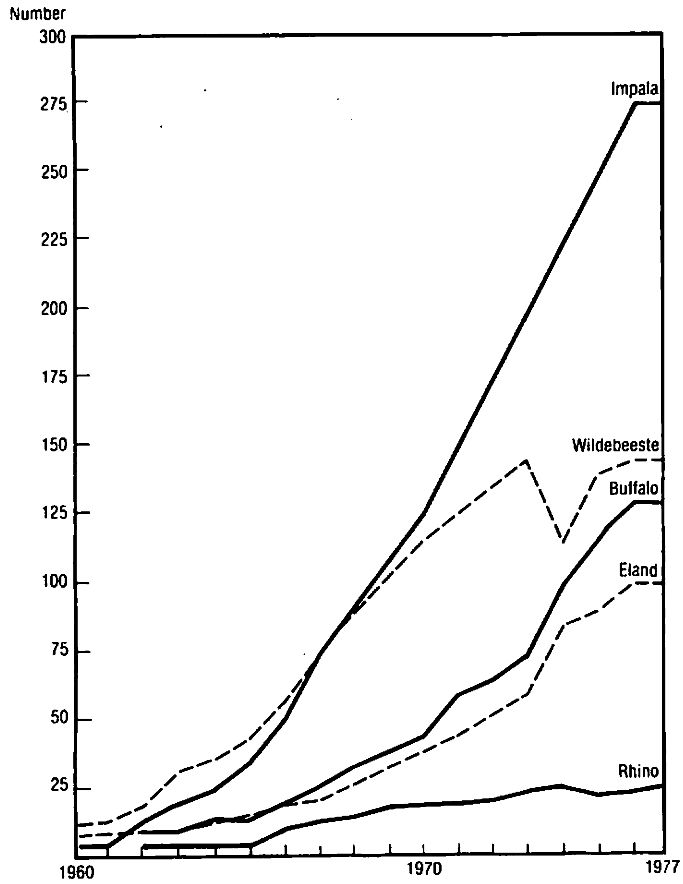

Fig. 1A Increase in numbers of five large ungulate species in the Whovi Wild Area of the Rhodes Matopos National Park, 1960 – 1977.

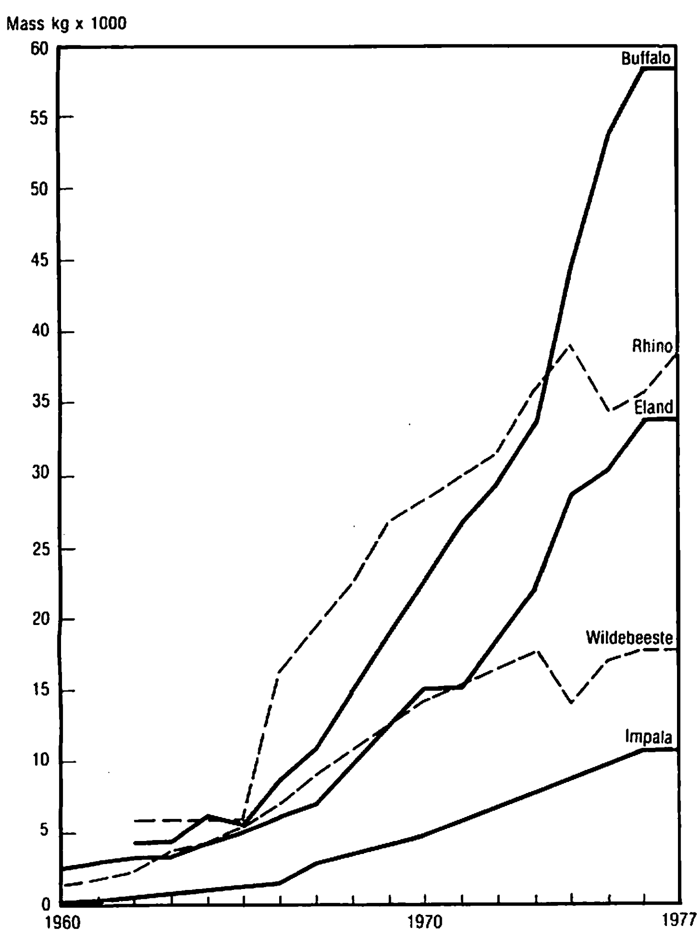

Fig. 1B Increase in biomass of five large ungulate species in the Whovi Wild Area of the Rhodes Matopos National Park, 1960 – 1977.

factor in their life history and may be reflected in their time of calving. From a survival point of view, calving should take place at a time when food nutrient levels are high and the food components available in the required form and in abundance so as to benefit the female with a calf at foot. High survival on this basis would result in the eventual development of a calving peak during a particular time of the year directly related to physical condition and food supply at that time.

Eland which were predominantly browsers in the Matopos calved during September when the trees were producing highly nutritious new shoots. Warthog farrowed in October at a time when they were largely feeding on the underground stems of *Cynodon dactylon*. Cumming (1975) shows a distinct seasonal change in diet of warthog indicating a large proportion of the diet between May and November to consist of rhizomes in the Sengwa area of Zimbabwe Rhodesia. It could be that the underground stems or rhizomes are highly nutritious and feeding on this source, for which there is little competition, is beneficial to the warthog. Tsessebe, wildebeest and impala calved during the initial phase of the wet season. These are low level grazers in Matopos and would be making use of the first grass flush which has a high percentage of crude protein (up to 25%) and low crude fibre (down to 25%) (Grobler 1978). Zebra, sable and buffalo which feed at the higher levels of the grass layer (although zebra can feed at the lower levels) calved at a time when the grasses are past the initial growth phase and are maturing.

In spite of peak mating taking place during the 'rut', males of at least some of the large ungulate species were sexually active throughout the year. A product of this are out of season calves, but one only has to look at a breeding male's activities to see that females are often checked by urinalysis for reproductive state. This strategy would cope with a possible change in out of season calf survival to eventually produce a new calving peak. A female sable born in February of a particular year, would have her first oestrus at either 15 months or 27 months of age which, in either case, would result in a February calf (Grobler 1978). Attainment of puberty is a function of the size of the mammal as well as its age (Sadleir 1969). High survival from calves born during a particular time would in most cases result in a repetition of the process, providing the gestation period is such that the time of conception to time of parturition results in calving taking place during the same time of year. This does in fact take place with the species discussed except giraffe and rhino which have gestation periods exceeding 12 months.

Standing crop and carrying capacity

The carrying capacity of African wildlife areas in terms of large herbivores standing crop is predicted by Coe *et al.* (1976), using the equation:

Log_{10} Large herbivore biomass = 1,685 (± 0,238) × Log_{10} annual rainfall − 1,095 (± 0,661).

Mean annual rainfall in the Matopos based on records collected since 1938 is 630 mm which gives a predicted large herbivore standing crop of 4 187 (+ 50) kg km^{-12}. The actual large ungulate standing crop was estimated as 2 181 kg km^{-2} where the total biomass of large ungulates

Table 3 Number of births recorded per month for 10 ungulate species in the Whovi Wild Area of the Rhodes Matopos National Park

Species	Month Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Total no. of births
Eland	–	–	13	28	1	2	–	–	–	–	–	–	44
Warthog	–	–	–	–	54	18	6	–	–	–	–	–	78
Tsessebe	–	–	3	–	6	11	2	1	1	–	–	–	24
Wildebeest	–	–	–	–	–	17	90	4	–	–	–	–	111
Impala	–	–	–	–	–	45	126	20	–	–	–	–	191
Zebra	–	–	–	–	–	1	1	4	7	–	–	2	15
Sable	–	–	–	–	–	–	1	13	31	16	4	–	65
Buffalo	–	–	–	–	–	1	–	6	9	44	9	–	69
White Rhino	5	1	–	–	2	–	1	–	2	5	2	7	25
Giraffe	–	1	1	–	1	1	1	1	1	–	1	1	9

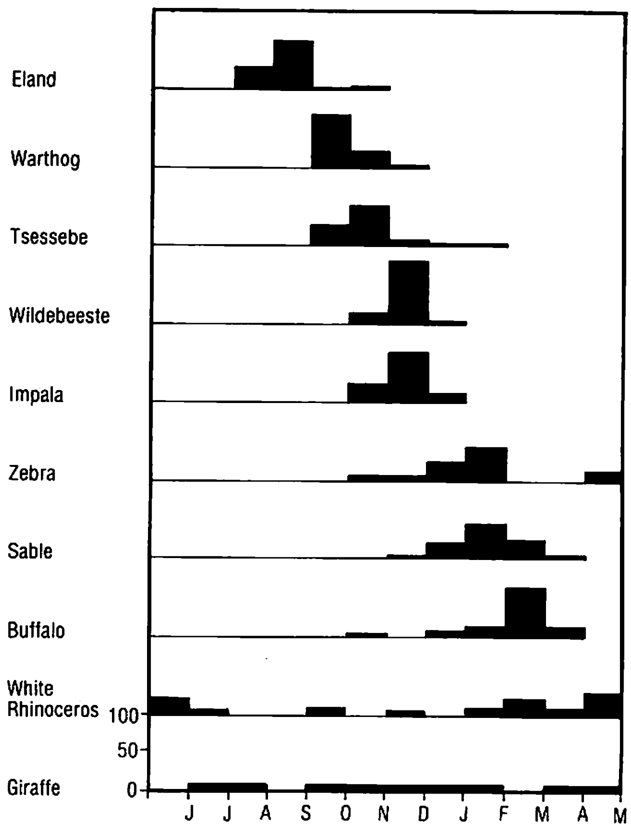

Fig. 2 Calving seasons of 10 large ungulate species in the Whovi Wild Area of the Rhodes Matopos National Park.

is 231 130 kg and the Whovi Wild Area is 105,97 km^2 giving a biomass of 2 187,1 kg km^{-2}.

Observations over the years showed that large ungulate species in the Whovi Wild Area made little use of the wooded kopjes, except possibly eland which browsed along their base. The eland and buffalo traversed the areas between the hills fairly extensively while the other species were relatively restricted in their movements through various habitat and social factors.

The area actually utilized by the large ungulates after deduction of the areas occupied by kopjes (53,54 km^2) and dams (0,53 km^2) is 51,90 km^2. This area was used to calculate a net large ungulate standing crop of 4 453 kg km^{-2} which is slightly higher than the predicted value but is a more realistic estimate of the standing crop in relation to carrying capacity, than the gross estimate using the entire area.

The granite kopjes and underlying rock formations of the Whovi Wild Area are such that effective annual precipitation and consequently primary productivity is increased by numerous perennial seeps and springs. This would raise the large ungulate carrying capacity of the area above that predicted by annual precipitation. Mean annual precipitation over the period 1973 to 1977 was 792 mm which may also serve to increase the standing crop above the carrying capacity estimate based on long term annual rainfall.

Relating large ungulate standing crop to carrying capacity is further complicated by the observation that five areas within the Whovi Wild Area are utilized to a greater extent than any other. These key areas (Fig. 3), defined as those areas most often occupied by the majority of the large ungulate community, consisted of lightly wooded grassland with patches of woodland and two of

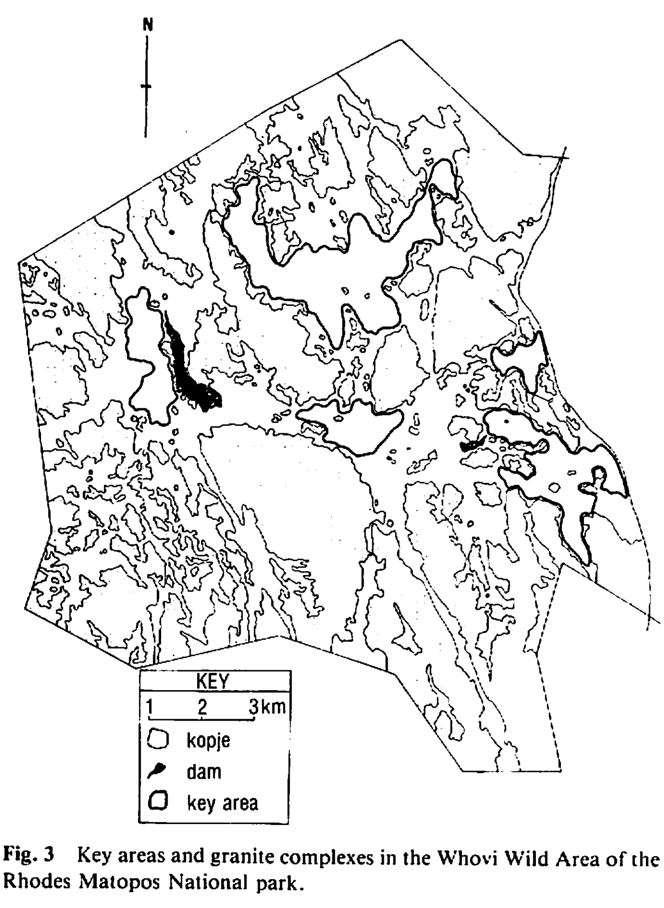

Fig. 3 Key areas and granite complexes in the Whovi Wild Area of the Rhodes Matopos National park.

them contained natural mineral licks. Their total area was only 14,18 km^2 or 13,38% of the Whovi Wild Area. An indication of the degree of utilization to which these areas may be subjected is provided by the October 1977 ground count which recorded 103 large ungulates of 13 species and 157 711 kg total biomass in them. This represented 68% of the total estimated biomass and reflects a standing crop of 11 112 kg km^{-2}.

Mentis (1977) shows that where large numbers of small ungulates are present biomass may underestimate standing crop. Since small animals expend more energy per unit mass than large animals, estimates of energy expenditure may provide a better measure of standing crop. Over 80% of the Matopos biomass under consideration is made up by large ungulates and for this reason the method used by Coe *et al.* was favoured.

Coe and his associates found a highly significant relationship between the energy expenditure of large herbivore communities and the annual precipitation. Their predictive equation for large herbivore carrying capacity in terms of energy expenditure is: Log_{10} Energy expenditure = 1,653 × Log_{10} Annual Rainfall — 0,341. Estimated energy expenditure by the large ungulate community was calculated as 19 331 kJh^{-1} km^{-2} for the 51,90 km^2 utilized portion of the Whovi Wild Area. This is 915 kJh^{-1} km^2 less than the predicted values. Using biomass as the measure of standing crop the six smaller ungulate species constitute 14,4% of the total whereas in terms of energy expenditure they constitute 22,4% of the standing crop.

Mentis (1977) pointed out that the carrying capacity of the veld is probably greater for larger ungulates which eat more roughage than it is for smaller ungulates with more specialized feeding habits. Bulk and roughage feeders improve the grazing for more specialized grazers. In the Whovi Wild Area the buffalo wander and feed extensively in the coarse grass areas opening them up for the more selective feeders. The data presented suggest that the population of species representing the majority of the large ungulate standing crop have reached a peak or have been maintained at a relatively stable level by translocation. The condition of the large ungulates was generally good as was the condition of the veld, including the more intensively utilized and therefore more sensitive key areas.

The value of the key area concept to management of large ungulate communities cannot be overstressed and it is suggested that habitat monitoring priorities should be specifically directed to these areas. The standing crop of the large ungulate community approximates the carrying capacity of the area as predicted by Coe *et al.* but the feeding strategies of different species may be important in maintaining a balance between them and the overall carrying capacity.

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