

Appendix A.

Calculation of the estimated food requirements and availability to the ungulate community in the river habitats during the drought years 1986-1987.

1. Ungulate numbers and age composition

Ungulate numbers along the Nossob and Auob rivers were recorded as described in Ground Counts.

Table A1. Total numbers of springbok, wildebeest, gemsbok and hartebeest along the Nossob and Auob river-beds in the KGNP during 1986 and 1987. CV=coefficient of variation.

Month/year	SPECIES			
	Springbok	Wildebeest	Gemsbok	Hartebeest
Mar 1986	7945	225	66	52
Apr 1986	4289	65	163	29
Jul 1986	5202	135	77	0
Dec 1986	8120	216	44	5
Feb 1987	5693	112	52	33
May 1987	5592	200	199	22
Jul 1987	3684	113	124	0
Oct 1987	2278	100	93	1
Dec 1987	9066	126	32	24
Mean ± SD	6096 ± 2444	144 ± 56	94 ± 57	18 ± 18
CV (%)	40,1	38,9	60,6	100,0

Table A2. Adult and juvenile (yearling and calf) ratios for springbok, wildebeest, gemsbok and hartebeest counted along the Nossob and Auob riverbeds in 1986 and 1987.

Species	Percentage adults	Percentage juveniles	Total number sexed
Springbok	69,3	30,7	18635
Wildebeest	71,5	28,5	1374
Gemsbok	82,5	17,5	1848
Hartebeest	78,9	21,1	157

Adult springbok, wildebeest, gemsbok and hartebeest body masses were assumed to be 39, 230, 200 and 140 kg respectively, using the averages for males and females from Skinner & Smithers (1990). Juvenile masses were taken as half adult mass.

2. Calculation of ungulate maintenance food requirements

Maintenance food requirements (R) (kg/day) of an individual animal was assumed to be equivalent to 3,0 % of body mass (ARC 1965). The estimated food requirements (F) of the total population of each species using the river habitats was calculated by :

$$F = R * 730 * T$$

where T = mass of the population in proportion to the age composition and 730 = number of days in two years (1986-1987).

As springbok are noted to graze predominantly in the summer months, switching to browse in the winter (Bigalke 1972; personal observations) their grass consumption was calculated for only six months per year.

The estimated requirements of the ungulate population were 3532992 kg/year (springbok = 2485286 kg/year; wildebeest = 622646 kg/year; gemsbok = 375694 kg/year; hartebeest = 49366 kg/year). But since wildebeest are restricted to within 15 km of fresh drinking water (Berry & Louw 1982b) (Appendix B), they therefore, would have used only 68,5 % of the river length. However as the other indigenous ungulate species were unaffected by drinking water (Mills & Retief 1984b), their distribution was assumed to be uniformly spread along the river, so only 68,5 % of their number would then have used the region principally used by the wildebeest. Therefore, the estimated total food requirement for the 'restricted area' was 2920577 kg/day.

3. The river productivity

The total area of the riverbed and riverside habitats along both rivers were 2.7 and 1,2 % of the KGNP, ie 247,6 and 110 km² respectively. The 'restricted area' amounted to 245 km².

Total productivity (P) (kg/years 1986 and 1987) of the grasses for the riverbed and riverside were estimated using:

$$P = (PR * AREA * 10) + (PS * AREA * 10)$$

where the productivity of the riverbed (PR) (g/m²/two years) was:

$$PR = (0,289x - 8,145) * MONTH$$

and the productivity of the riverside (PS) (g/m²/two years) was:

$$PS = (0,089x - 2,30) * MONTH$$

where x = monthly rainfall in mm, MONTH = the number of months with rainfall greater than the zero yield value in 1986 and 1987, AREA = habitat area in hectares and 10 = conversion of g/m^2 to kg/ha . The zero yield rainfalls for the riverbed and sides were 28 and 25 mm respectively. Over the 1986 and 1987 summer seasons only three months: December 1985 (37,7 mm), November 1986 (43,6 mm) and February 1987 (47,6 mm) had mean monthly rainfalls in excess of the zero yields. Rainfall was recorded at seven stations along the two rivers.

The total productivity of the entire length of the river in the KGNP was estimated as 3636035 kg in 1986 and 1987, and for the 'restricted area' was 2490683 kg.

Therefore the maintenance requirements of the ungulate community along the fossil Nossob and Auob rivers was 97,3 % of the total river grass production or 117,3 % of the 'restricted area' in the 1986 and 1987 drought years.

	Estimated total	95%	Estimated total	95%
Jan 74	4281	1458	1228	1183
Apr 75	4039	1276	171	166
Feb 78	4281	1429	248	241
Aug 78	240	5813	1199	853
Mar 79	6715	2785	566	550
Aug 79	150	1685	1385	115472
Mar 80	7022	1765	458	445
Aug 80	153	8659	1802	1630
Apr 81	10885	2154	784	624
Sep 81	134	11699	2104	1071
Mar 82	5153	1960	1117	1067
Aug 82	127	10607	2288	1288
May 83	12899	2893	792	769
Sep 83	155	6111	1536	675
Jan 84	9465	2389	1208	1425
Sep 84	187	9410	2178	1640
Mean(1974-84)	7316		6530	
SD	2895		5734	
CV	38,7		87,8	
n	20		20	
Mean(1974-89)	8088		743	
SD	2910		482	
CV	35,9		64,8	
n	30		30	

Excluding Aug 79 and Sep 85 wildebeest immigrations and the low Nov 89 count.

Appendix B.

Table B1. Extrapolated aerial census population estimates for gemsbok and wildebeest in the KGNP between 1974 and 1984, with summer (November-April) rainfall. CV=coefficient of variation (%); 95%=95% confidence limits; SD=standard deviation.

Survey Month/ year	Rainfall	Gemsbok		Wildebeest	
		Estimated total	95%	Estimated total	95%
Apr 74		6781	2458	1226	1169
Aug 74	560	4257	1104	263	256
Apr 75		4039	1276	171	166
Aug 75	228	6364	2149	244	237
Apr 76		5664	1404	237	229
Jul 76	522	4644	1213	79	75
Feb 78		4281	1429	248	241
Aug 78	240	5813	1199	1436	853
Mar 79		8715	2785	566	550
Aug 79	150	3685	1385	115472	40192
Mar 80		7022	1765	458	445
Aug 80	153	8659	1802	1630	1045
Apr 81		10989	2154	784	624
Sep 81	134	11699	2104	1071	1040
Mar 82		5152	1960	1117	1067
Aug 82	127	10607	2288	1288	1251
May 83		12899	2893	792	769
Sep 83	155	6111	1536	675	656
Jun 84		9465	2389	1208	1425
Sep 84	187	9410	2278	1640	1302
Mean(1974-84)		7316		6530	
SD		2805		5734	
CV		38,7		87,8	
n		20		20	
Mean(1974-89)		8088		743*	
SD		2910		482	
CV		35,9		64,8	
n		30		30	

*Excluding Aug 79 and Sep 85 wildebeest immigrations and the low Nov 89 count.

The importance of borehole water and lick sites to Kalahari ungulates

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The utilization by ungulates of two artificial waterholes supplied with borehole water of different quality was studied. The ungulates showed a preference for the fresher water. Blue wildebeest (*Connochaetes taurinus*) were found to be the most water-dependent species, while springbok (*Antidorcas marsupialis*), gemsbok (*Oryx gazella*), red hartebeest (*Alcelaphus buselaphus*) and steenbok (*Raphicerus campestris*) showed greater use of mineral lick sites at waterholes than of the water itself. The differences are probably due to the various abilities of the ungulate species to survive without drinking water, the mineral status of preferred habitats and ungulate feeding habits.

The southern Kalahari is a vast semi-desert region consisting predominantly of red sand overlying a calcareous sandstone layer. The red sandy soils are notably infertile, being relatively free of soluble salts and low in exchangeable cations, and produce poor quality vegetation (Leistner, 1967; Van Rooyen, 1984). The calcrete is exposed within the pans and dry riverbeds, has white, more fertile soils and a vegetation of better nutritional quality (Leistner, 1967). These finer, white soils have a higher concentration of soluble salts, more exchangeable cations, consisting principally of sodium, calcium, magnesium and potassium and a greater clay component. The dry riverbeds are the most utilized habitat within the parks supporting large seasonal concentrations of springbok (*Antidorcas marsupialis*), gemsbok (*Oryx gazella*), blue wildebeest (*Connochaetes taurinus*) and red hartebeest (*Alcelaphus buselaphus*) (Mills & Retief, 1984a). Eland (*Taurotragus oryx*), steenbok (*Raphicerus campestris*) and the common duiker (*Sylvicapra grimmia*) confine themselves predominantly to the sandveld habitats and infrequently utilize the riverbeds (Van der Walt, Retief *et al.*, 1984).

No natural permanent surface water exists within the region; pans and dry riverbeds hold water for short periods after sporadic heavy rainstorms. The indigenous Kalahari ungulates are generally able to survive without drinking water because of their behavioural and physiological adaptations (Taylor, 1968; Maloiy & Hopcraft, 1971; Lewis, 1977; Louw, 1984; Williamson, 1987). Yet an ability to roam widely in search of better quality food patches to satisfy water and energy demands may be a most important adaptation, particularly for the large ungulates.

Over the last century man's increased pressure on the Kalahari has reduced the indigenous ungulates' natural ranges to predominantly within wildlife sanctuaries and safari areas (Campbell, 1981). As drinking water was considered necessary within the region (Van Wyk & Le Riche, 1984), artificial waterholes fed with borehole water of

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variable quality have been erected within the Kalahari Gemsbok National Park since the 1930s. The usefulness and effect of this practice has been the subject of much speculation and controversy (Mills & Retief, 1984b). Most of the indigenous ungulate species can utilize mineralized water to a certain extent (Child, Parris & le Riche, 1971) but whether the water or lick sites are the main attractions is not known. The importance to Kalahari ungulates of lick sites, situated predominantly on pans and exposed calcrete has been noted by Weir (1969, 1972), Parris & Child (1973), Kreulen & Jager (1984) and Kreulen (1985).

The aim of this study was to determine the relative importance of lick sites and drinking water of different qualities to the various ungulate species, in relation to their habitat preferences and feeding habits. It was hypothesised that ungulate species that utilize browse and associate more with the mineral deficient red sand habitats, practise more geophagia than those species that predominantly graze and prefer habitats on the mineral richer white soils.

Study area

The study was undertaken in the Kalahari Gemsbok National Park (KGNP) of South Africa which adjoins the Gemsbok National Park (GNP) of Botswana. Two dry riverbeds, the Auob and Nossob, run through the KGNP, the latter demarcating the boundary of the two parks. Rainfall isohyets range from 150 mm in the south-west of the KGNP to 300 mm in the north-east of the GNP. Most rain falls in the summer from November to April with 70 per cent received between January and April (Knight, unpublished data).

The potable (fresh) Cubitje Quap (CQ) and non-potable (mineralized) Kousaunt (KS) waterholes, both served by windmills and 44 km apart on the dry Nossob river, were chosen for the study. At KS, water was pumped into a fibre-glass storage tank which pressure fed a ball-valve controlled trough. Overflow from the storage tank usually formed a puddle at its base. CQ water was pumped directly into a concrete trough, and occasionally overflowed forming small pools. For purposes of comparison the 'trough' at CQ was equated with the storage tank at KS. The licks created at both sites from evaporation of overflow water were in such a position that water no longer inundated them.

Methods

Water samples were taken from the storage tank, trough and overflow at Kousaunt (KS) and from the trough and overflow at Cubitje Quap (CQ) waterholes in October 1984. The samples for chemical analyses were collected in glass bottles without the addition of preservatives, and analysed within 2 weeks of collection using the standard analytical methods employed by the National Institute for Water Research (NIWR) (Smith, 1983; Siebert, 1985).

Soil samples were collected from actively used lick sites near the two waterholes; non-lick soil samples were taken randomly from the surrounding soil at the same depth as at the exposed lick sites but from at least 5 m away. Extracts of saturated pastes of the samples (Buys 1980) were analysed for: potassium, calcium, magnesium, sulphate, chloride and carbonate ions, pH and conductivity. Phosphorus was extracted according to the Bray no. 2 method (Bray & Kartz, 1945).

Single 24 h observation periods were undertaken monthly over full moon at each of the two waterholes from March 1984 to April 1985. The instantaneous scan sampling method (Lehner, 1979) with a 5-minute interval was used, recording all ungulates within 50 m of the waterhole. The numbers drinking, practising geophagia and other activities (lumped into one category) were recorded, in addition to the numbers drinking from the storage tank, overflow and trough. Observations were made from a vehicle situated within 300 m

of the waterholes during the day and 100 m at night. Rainfall was monitored monthly from rain gauges at Nossob (NS) and Groot Brak (GB) that were within 10 km of CQ and KS, respectively.

Ungulate numbers within the Nossob riverbed 10 km north and south of the two study waterholes were extracted from regular game counts ($n = 10$) undertaken during the study. Counts of all ungulates seen along the same route were made from a slow moving vehicle, as done by Bothma & Mills (1977).

Selection for habitats on white or red soils by the different ungulate species (except steenbok) was determined from radio-collared animals. All radio-collared animals (16 gemsbok, 10 wildebeest, three hartebeest and five springbok) were located approximately once every 2–3 weeks over the study period; sand types and habitats on which they occurred were noted. Use of habitats on white and red sand by steenbok were determined from monthly ground counts ($n = 10$) undertaken along the same routes in the Nossob and Auob riverbeds (422 km) and within the dunes (247 km) using the same methods mentioned above. A habitat preference index (HPI) was calculated by the division of the percentage occurrence of white and red sand habitats into the percentage occurrence of the specific ungulate species in those habitats.

Where more than two samples were available all data are presented as means with standard deviation (S.D.). Differences between means were initially tested using analysis of variance (F test) (Cass, 1973). Welkowitz, Ewen *et al.* (1971) was followed for the determination of Student's *t*-test, while for non-parametric data the Mann-Whitney (U), Chi-squared, and Wilcoxon matched pairs (T) were used (Siegel, 1956). Percentile data were analysed using arcsine transformations (Sokal & Rohlf, 1982). Regression equations were calculated by the method of least squares (Cass, 1973). The minimum accepted level of significance was taken as $p < 0.05$.

Results

Water analyses

KS water was found to be approximately six times as mineralized as CQ water (Table 1). KS water increased in concentration from 1.2% total dissolved solids (TDS) in the storage tank to 1.5 and 3.5% TDS in the overflow and trough, respectively, while CQ's water was much more potable (0.2% TDS) with little difference between the storage tank and overflow water concentrations.

Sodium had the highest concentrations of all the ions tested for at both sites, followed by the chloride and sulphates, respectively (Table 1). Sodium, calcium, sulphate, chloride and fluoride ion concentrations of KS storage tank water averaged seven times greater than CQ water, while the nitrate and phosphate levels were lower than that found in the CQ water. All the ions (except calcium, nitrates and nitrites) increased in concentration from the storage tank to overflow and trough, at KS.

Soil analyses

Sodium, sulphate and chloride ions were found to be the most concentrated ions in both lick and control soils at both sites (Table 2). KS soils had generally higher concentrations of all ions, except phosphorous. The sodium, sulphate and chloride ion concentrations of the lick sites at both CQ (Chi-squared = 37.0; D.F. = 1) and KS (Chi-squared = 28.58; D.F. = 2) waterholes were significantly more concentrated than that found in the surrounding control soils, while the remaining ions showed the reverse tendency.

Table 1. Results of chemical analyses of filtered water collected at Cubitje Quap (CQ) and Kousaunt (KS) waterholes in the Kalahari Gemsbok National Park

Waterhole	Collection site	pH	Elect. Cond. (ms/m)	mg·l ⁻¹								µg·l ⁻¹	
				Na	Ca	NO ₃ + NO ₂	NO ₂	SO ₄	PO ₄	PO ₄ ³⁻	Cl	F	TDS (ppm)
KS	reservoir	8·81	2460	4465	35	9·6	0·4	3493	< 0·2	< 0·2	4295	4000	12300
	overflow	9·25	3340	5677	11	0·4	0·4	4505	< 0·2	< 0·2	5732	5000	15930
	trough	9·14	7880	10830	18	0·3	0·3	10228	1·4	1·0	13370	6800	34460
CQ	reservoir	8·96	405	755	5	20·3	3·1	414	1·7	0·2	429	815	1630
	overflow	9·17	444	824	6	19·8	< 0·1	519	1·6	0·3	471	950	1840

Table 2. Results of soil analyses from lick and non-lick sites at Cubitje Quap (CQ) and Kousaunt (KS) waterholes in the Kalahari Gemsbok National Park

Waterhole	Site	pH (H ₂ O)	Resistance (ohm)	Soluble components in saturation extract							
				Ca	Mg	K	Na	SO ₄	Cl	Bray ii P	CO ₃
				mg l ⁻¹							mg kg ⁻¹
KS	non-lick	9·22	180	190	26	60	1375	1804	237	133	+
	lick	9·02	55	364	53	204	7105	10866	1737	263	+
CQ	non-lick	9·40	600	132	12	36	504	752	117	155	+
	lick	9·83	100	73	8	27	1810	1910	241	137	+

Ungulate counts

Significantly (Chi-squared = 194; $p < 0.025$) more animals visited CQ than KS, with only springbok and wildebeest showing a preference for CQ over KS (Table 3). This probably resulted from greater numbers of these two species in the CQ region (Table 4). More gemsbok ($U = 15$; $p < 0.01$) visited KS than CQ and similarly more gemsbok were in the vicinity of that waterhole.

CQ had generally greater proportions of ungulates visiting the water-hole over 24 h in relation to the mean strip count totals (Table 5), than did KS. The springbok ($U = 28$; $p < 0.05$) and hartebeest ($U = 24$; $p < 0.01$) appeared to show an aversion for the KS water-hole (Tables 3 & 4). There appeared to be no seasonal differences in the numbers of animals visiting the waterholes (Table 6).

Table 3. Mean (\pm S.D.) number of ungulates visiting Cubitje Quap (CQ) ($n = 13$) and Kousaunt (KS) ($n = 12$) waterholes over 24 h

Species	CQ number	KS number	Test
Springbok	404.0 \pm 467.7	74.4 \pm 125.7	$U = 15$; $p < 0.01$
Wildebeest	28.2 \pm 37.8	7.6 \pm 16.0	$U = 15.5$; $p < 0.01$
Gemsbok	2.5 \pm 8.5	3.7 \pm 6.6	$U = 15$; $p < 0.01$
Hartebeest	1.2 \pm 1.7	1.9 \pm 6.0	$U = 30$; $p > 0.05$
Steenbok	0.8 \pm 1.0	0.5 \pm 0.5	$U = 65.7$; $p > 0.05$

Table 4. Mean (\pm S.D.) number of ungulates counted in 10 counts along the Nossob riverbed in a strip 10 km north and south of Cubitje Quap (CQ) and Kousaunt (KS) waterholes

Species	CQ number	KS number	Test
Springbok	423.2 \pm 226.1	311.8 \pm 523.3	$U = 15$; $p < 0.05$
Wildebeest	404.9 \pm 54.5	7.6 \pm 16.6	$U = 15.5$; $p < 0.05$
Gemsbok	0.5 \pm 0.5	2.9 \pm 3.2	$U = 15.5$; $p < 0.05$
Hartebeest	2.9 \pm 3.0	22.5 \pm 38.4	$U = 30$; $p > 0.05$

Table 5. Mean percentage of ungulates visiting the waterholes over 24 h in relation to the number in a 10 km strip north and south of the waterholes

Species	Percentage visiting Cubitje Quap	Percentage visiting Kousaunt
Springbok	95.7	4.5
Wildebeest	75.1	82.9
Gemsbok	506.1	131.0
Hartebeest	41.4	8.0

Table 6. Mean (S.D.) number of ungulates visiting the two waterholes over 24 h in summer and winter in the KGNP

Species	Summer mean	Winter mean	Test
Springbok	323.0 ± 461.0	131.0 ± 176.6	U = 11; p > 0.11
Wildebeest	38.4 ± 32.9	38.8 ± 62.7	t = 0.02; p > 0.05
Gemsbok	4.5 ± 4.3	9.6 ± 9.0	t = 0.95; p > 0.05

Utilization of borehole water and lick sites

A gradation from steenbok to wildebeest with respect to drinking and geophagia were found at both waterholes (Fig. 1). No significant intraspecific differences between the relative proportions drinking and practising geophagia at each site were found which justified lumping waterhole data for interspecific comparisons.

Steenbok and wildebeest practised significantly the most and least geophagia, respectively, while no significant differences existed between the intermediate springbok, gemsbok and hartebeest species (Fig. 1). At each waterhole preferred drinking sites were noted. Springbok (U = 37; D.F. = 12) and wildebeest (U = 3; D.F. = 11) favoured the trough water at CQ while the other species selected for the overflow. At KS a significant (Chi-squared = 62.29; D.F. = 3) preference for the fresher overflow water was found, except for springbok and steenbok (the latter of which did not drink at all).

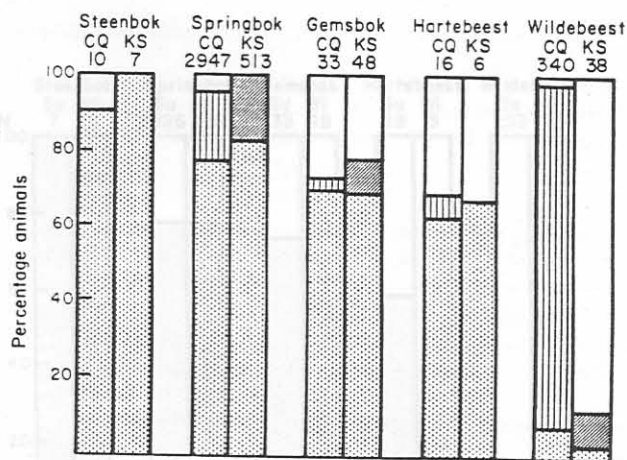


Figure 1. The numbers and proportions of the five different ungulate species drinking and practising geophagia at the potable Cubitje Quap (CQ) and mineralized Kousaunt (KS) waterholes. Geophagia; Drink; Other activities; Overflow; Trough.

From Fig. 2 it is evident that springbok, hartebeest and wildebeest performed a greater proportion of other activities around the waterholes than did gemsbok and steenbok. This probably results from the first three species frequenting the waterholes in significantly larger group sizes of 28.4 ± 38.8 ($n = 216$), 8.6 ± 16.4 ($n = 15$) and 3.0 ± 5.1 ($n = 58$), respectively, in comparison to the smaller groups of 2.7 ± 1.8 ($n = 37$) and 1.0 ± 0.0 ($n = 14$) for gemsbok and steenbok, respectively.

No significant seasonal differences existed in the proportion of each species that drank and practised geophagia at the waterholes (Fig. 3). However, only sufficient data on the

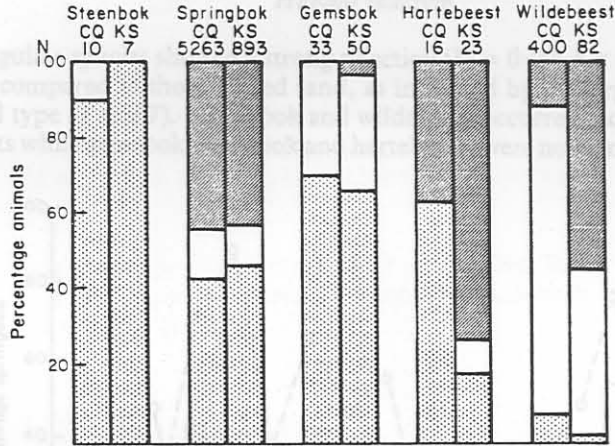


Figure 2. The numbers of five different ungulate species drinking, practising geophagia and other activities at the potable Cubitje Quap (CQ) and mineralized Kousaunt (KS) water-holes. ▨, geophagia; □, drink; ▩, other activities.

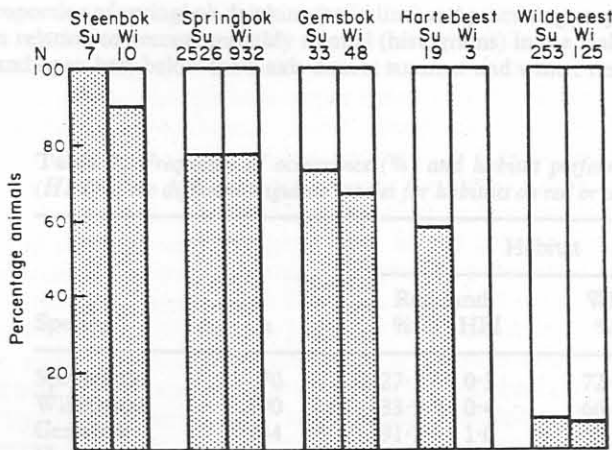


Figure 3. Seasonal variation (Su = summer; Wi = winter) in the proportions of springbok, wildebeest and gemsbok drinking and practising geophagia at two waterholes in the Kalahari Gemsbok National Park. ▨, geophagia; □, drink.

monthly variation of the two behaviours was obtained for springbok. The combined data from the two waterholes indicated that a pattern in drinking and geophagia existed (Fig. 4). Peaks in geophagia coincided with high rainfall months (April 1984 and March 1985), while peaks in drinking occurred in hot dry months (March 1984 and October 1985) that were preceded by at least a month of similar hot, dry conditions. Rainfall showed a relatively strong positive correlation ($r = 0.53$) with the number of springbok practising geophagia, while a weaker negative correlation ($r = -0.11$) with drinking was noted. Geophagia by springbok showed a relatively strong, negative correlation ($r = -0.47$) with drinking for the year's data. However, seasonally, a stronger positive correlation between geophagia and drinking was noted in the summer ($r = 0.76$) than in the winter ($r = -0.22$).

Habitat selection

The five ungulate species showed a strong selection ($U = 0.00$; $p < 0.004$) for habitats on white sand compared to those on red sand, as indicated by the larger HPI values of the former sand type (Table 7). Springbok and wildebeest occurred more often within white sand habitats while gemsbok, steenbok and hartebeest, were noted more frequently in red

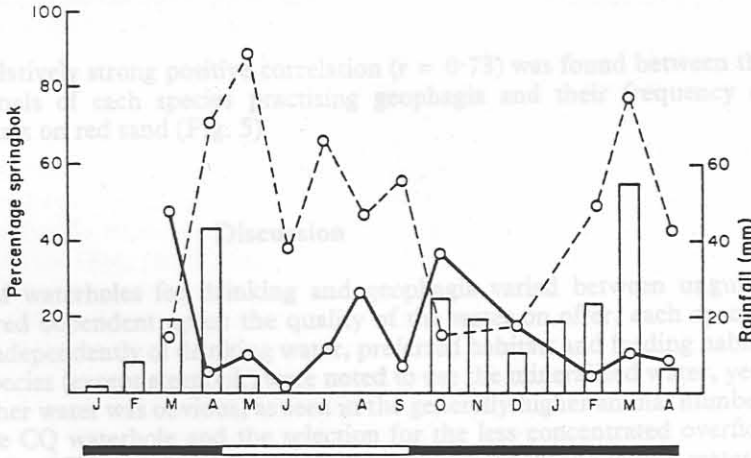


Figure 4. Proportion of springbok drinking (solid line) and practising geophagia (dotted line) at two waterholes in relation to average monthly rainfall (histograms) in the Kalahari Gemsbok National Park. Solid and open bars below the x-axis denote summer and winter respectively.

Table 7. Frequency of occurrence (%) and habitat preference index (HPI) of the different ungulate species for habitats on red or white sand

Species	n	Habitat			
		Red sand		White sand	
		%	HPI	%	HPI
Springbok	70	27.1	0.3	72.9	18.2
Wildebeest	190	33.9	0.4	66.1	16.5
Gemsbok	244	91.7	1.0	8.3	2.1
Hartebeest	30	78.6	0.8	21.4	5.4
Steenbok	567	91.2	1.0	8.8	2.2

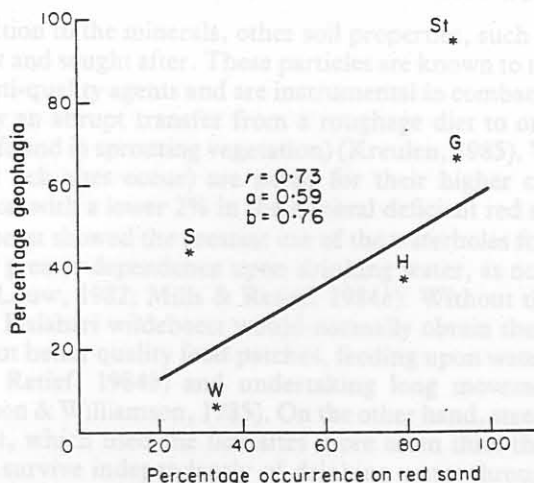


Figure 5. Relationship between the proportion of ungulate species practising geophagia and their occurrence in red sand veld habitats. G, gemsbok; H, red hartebeest; S, springbok; St, steenbok; W, blue wildebeest.

sand habitats. A relatively strong positive correlation ($r = 0.73$) was found between the proportion of animals of each species practising geophagia and their frequency of occurrence in habitats on red sand (Fig. 5).

Discussion

The importance of waterholes for drinking and geophagia varied between ungulate species and appeared dependent upon: the quality of the water on offer, each species' ability to survive independently of drinking water, preferred habitats and feeding habits. All the ungulate species (except steenbok) were noted to use the mineralized water, yet a preference for fresher water was obvious, as seen in the generally higher animal numbers visiting the potable CQ waterhole and the selection for the less concentrated overflow water at the mineralized KS waterhole. Consumption of the overflow and trough water at KS may be hazardous to an animal's health as their respective concentrations were within, and exceeded, the tolerance levels of 1.3–1.7% total dissolved solids (TDS) recommended for domesticated ungulates (Church, 1979). In addition, the sodium sulphate and sodium chloride concentrations approached the safe upper limits of 2.0 and 1.5%, respectively, recorded for livestock (NCR, 1974; Church, 1979). However, within the licks where the same salts were predominant, no concentration greater than 1.8 and 0.9% were found, which would make the lick sites a more healthy source for these required minerals.

Sodium is probably the mineral in demand from the licks; at both lick sites, sodium and its anions sulphate and chloride were in significantly higher concentrations than in the surrounding control soils. This has been similarly noted in other areas of the Kalahari (Weir, 1969; 1972; Kreulen & Jager, 1984; Kreulen, 1985) and elsewhere (Blair-West, Coghlan *et al.*, 1968; Weir, 1973; Belovsky & Jordan, 1981; Tankersley & Gasaway, 1983; Watts & Schemnitz, 1985). A shortage of sodium, as is characteristic of tropical forages (McDowell, Conrad *et al.*, 1984) and notably so within the Kalahari (Weir, 1972; DHV, 1980), is of great importance particularly to ruminants inhabiting hot arid regions. Compensatory excretion of sodium via the kidneys and/or sweat glands safeguards plasma and extracellular osmotic conditions. This allows the ruminant to endure considerable dehydration (Maloiy, MacFarlane *et al.*, 1979).

In addition to the minerals, other soil properties, such as clay particles are considered important and sought after. These particles are known to neutralize the effects of tannins, absorb anti-quality agents and are instrumental in combating acidosis (a gastric condition caused by an abrupt transfer from a roughage diet to one high in fermentable soluble sugars as found in sprouting vegetation) (Kreulen, 1985). White riverine and pan soils (on which all lick sites occur) are noted for their higher clay proportions of 20–22% in comparison with a lower 2% in the mineral deficient red soils (Leistner, 1967).

Wildebeest showed the greatest use of the waterholes for drinking, which reflects their relatively greater dependence upon drinking water, as noted elsewhere (Western, 1975; Berry & Louw, 1982; Mills & Retief, 1984b). Without the provision of artificial waterholes the Kalahari wildebeest would normally obtain their water requirements through seeking out better quality food patches, feeding upon water storage plants such as melons (Mills & Retief, 1984b) and undertaking long movements to natural water sources (Williamson & Williamson, 1985). On the other hand, steenbok, springbok, gemsbok and hartebeest, which used the lick sites more often than they drank, are known for their ability to survive independently of drinking water through effective physiological, and behavioural adaptations (Taylor, 1968; Maloiy & Hopcraft, 1971; Lewis, 1977; Stanley-Price, 1978; Louw, 1984; Smithers, 1983; Williamson, 1987). These species, unlike the wildebeest, are also more selective feeders (Jarman, 1974) and hence able to more precisely choose better quality food items.

The degree to which a species practices geophagia appears closely linked to the mineral status of its preferred habitat and the species feeding habits. Species, such as steenbok, gemsbok and hartebeest (Table 7) that occurred more frequently in habitats on the mineral-deficient red sands, would be exposed to a poorer quality vegetation (Leistner, 1967; Van Rooyen, 1984). Hence they practised more geophagia to supplement their mineral intake than would species such as wildebeest that occurred more frequently within the better quality white sand habitats. The degree to which a species utilizes browse complicates the idea; geophagia, and particularly the consumption of clay particles, is suggested to be advantageous in neutralizing the effects of secondary compounds (Kreulen, 1985). Woody plants, and particularly those on infertile soils (such as the red Kalahari sands) are known for their characteristically high tannin levels (Watermann, Mbi *et al.*, 1980). This would explain why steenbok and springbok, both extensive browsers (Bigalke, 1972; Smithers, 1983) practised more geophagia in comparison with the other species, all of which are bulk roughage feeders (Hofmann & Stewart, 1972). The combination of a high occurrence in red sand habitats and browsing by steenbok accounts for their high proportion of geophagia. Similarly, the gemsbok's frequent occurrence on red sands and limited use of browse (Dieckmann, 1980; Smithers, 1983; Knight, unpublished data) places it in an intermediate position with respect to geophagia (Fig. 2). Hartebeest, which only graze (Stanley-Price, 1978) and frequent the red sands less (Table 7), practised geophagia to a lesser extent. At the extreme of the scale, wildebeest which only graze (Attwell, 1977; Knight, unpublished data) and showed a greater affiliation with white sand habitats practised the least geophagia of the five ungulate species.

Rainfall also appears to influence geophagia. Peaks of geophagia by springbok that coincided with high rainfall months (Fig. 3) gives credence to the hypothesis of Blair-West, Coghlan *et al.* (1968) that geophagia buffers the effect of acidosis. However, the use of lick sites throughout the year by all species results from a general deficiency of minerals within the Kalahari ecosystem.

In conclusion, the present study shows that the indigenous ungulates of the Kalahari will use fresh water in preference to mineralized water. It also reveals that wildebeest are the most water-dependent ungulate species and that the less water-dependent species are attracted more to the waterholes for the lick sites than the water itself. The use of these lick sites depends upon the species' feeding habits and the degree of association with mineral-deficient soils.

Summary

The indigenous Kalahari ungulates were found to use mineralized borehole water, yet a preference by all species for the freshest water on offer was noted. Blue wildebeest were found to be the most water-dependent species. Their grazing habits and greater association with habitats on the mineral richer white soils are suggested to explain their limited use of the mineral licks. The more water-independent steenbok, springbok and gemsbok that utilized browse and associated more with the mineral-deficient red Kalahari sands were found to frequent the mineral licks more often. The grazing hartebeest that similarly used the red sands were intermediate between the wildebeest and steenbok, springbok and gemsbok group with respect to geophagia. Geophagia is suggested to be beneficial in supplementing deficient minerals (particularly sodium), combating anti-quality agents and neutralizing the effects of acidosis.

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