

## CHAPTER 7

### POPULATION DYNAMICS

#### Introduction

A species' ability to survive in an area primarily depends upon its members' ability to maintain sufficient rates of nutrient intake. The success of this is in turn reflected in survival, growth and reproductive rates of the population. Thus studies of population dynamics reflect on the physiological and reproductive reaction of population members to various extrinsic (such as climate, predators and disease) and intrinsic or density-dependent (such as reduced fecundity, natality, population size) factors. It is commonly accepted in large herbivore species that extrinsic factors, such as food availability, regulate population numbers (Klein 1968, Coe *et al.* 1976, Sinclair 1977, Fryxell 1987a). But as population density increases, intrinsic factors such as diminished fecundity and increased mortality become increasingly important (Sinclair 1979, Clutton-Brock *et al.* 1982). Thus the two basic forms of regulation are not separate mechanisms but additive, operating effectively at different population densities (Caughley & Krebs 1983), creating in many circumstances a rather complicated picture owing to the multitude of interactions and influence of unpredictable environmental fluctuations (May 1989). A study of population dynamics provides an overview of these changes.

Population sizes usually rise in response to increases in food or habitat availability (Klein 1968, Pellew 1983, Fryxell 1987a) or reduced incidence of predation and disease (Sinclair 1977). Variation in the food supply is directly correlated with climatic variables, and particularly with rainfall at low altitudes (Sinclair 1975, Seely 1978, Chapter 3). Thus, in the southern Kalahari where rainfall is erratic in time and space, ungulate populations are expected to fluctuate directly with the food supply and indirectly with rainfall. However, the extent to which populations are expected to fluctuate depends on each species' physiological and behavioural adaptations to the harsh environment. Therefore

a species such as blue wildebeest which is at the southwestern limit of its distribution in the southern Kalahari (Smithers 1983) and whose permanent residence is maintained through the provision of drinking water (Mills & Retief 1984a) is expected to be less well adapted than the permanent resident, the gemsbok, to the harsh conditions. These differences are expected to be manifested in population variables such as density (Fryxell 1987a), group sizes (Jarman 1974, Southwell 1984, Wachter 1986), body condition (Berry & Louw 1982a) and sex and age composition (Sinclair 1977, Fryxell 1987b) in relation to rainfall over a number of years.

## Results

### Aerial Surveys

#### Perception Correction Factors

Perception correction factors for gemsbok determined from three strip widths were incorporated into density estimates of the 1988 and 1989 census results (Table 50). As no significant differences existed between strip widths ( $F=2,92$ ;  $df=3 \text{ \& } 6$ ;  $P>0,05$ ) and surveys ( $F=1,11$ ;  $df=2 \text{ \& } 6$ ;  $P>0,05$ ) a mean perception correction factor of  $1,0678 \pm 0,033$  ( $\pm SD$ ) was used in adjusting previous gemsbok census results.

As only  $55,5 \pm 39,6$  ( $\pm SD$ ) wildebeest in  $2,5 \pm 1,0$  ( $\pm SD$ ) groups per survey were counted in the 1988 and 1989 censuses, the data were considered insufficient to calculate specific perception correction factors for wildebeest. Therefore, mean perception correction factors for large bodied species (wildebeest, eland, gemsbok, red hartebeest and ostrich) for 100 m, 300 m and 500 m were calculated and used to adjust wildebeest counts for each survey (Table 51). Adjustment of surveys previous to 1988 were based on a mean perception correction factor of  $1,0793 \pm 0,0360$  ( $\pm SD$ ) as no differences existed between surveys ( $F=3,93$ ;  $df=3 \text{ \& } 6$ ;  $P>0,05$ ) and strip widths ( $F=1,23$ ;  $df=2 \text{ \& } 6$ ;  $P>0,05$ )

Table 50. Perception correction factors (C) and their coefficients of variation (Cp) for gemsbok in three strip widths from four aerial surveys conducted in 1988 and 1989 in the KGNP. N = total number seen.

Survey		Strip		Width (m)			
		100	N	300	N	500	N
May 88	C	1,0671	202	1,0906	501	1,292	876
	Cp	(0,011)		(0,008)		(0,010)	
Oct 88	C	1,0416	192	1,0457	478	1,0496	744
	Cp	(0,006)		(0,005)		(0,004)	
Jul 89	C	1,1101	387	1,0501	635	1,0854	1330
	Cp	(0,015)		(0,004)		(0,006)	
Nov 89	C	1,0122	218	1,0530	271	1,0790	326
	Cp	(0,003)		(0,007)		(0,001)	
Mean ± SD	C	1,0579 ± 0,021		1,0599 ± 0,021		1,0858 ± 0,033	

Table 51. Mean perception correction factors (C) and their coefficients of variation for large bodied animals (gemsbok, wildebeest, hartebeest, eland and ostrich) for three strip widths in four surveys in 1988 and 1989 in the KGNP.

Survey		Strip Width (m)		
		100	300	500
May 88	C	1,0795	1,1049	1,1476
	Cp	(0,012)	(0,010)	(0,236)
Oct 88	C	1,0802	1,0819	1,0747
	Cp	(0,010)	(0,007)	(0,005)
Jul 89	C	1,1185	1,0512	1,0983
	Cp	(0,002)	(0,004)	(0,014)
Nov 89	C	1,0151	1,0359	1,0636
	Cp	(0,002)	(0,004)	(0,006)
Mean ± SD		1,073 ± 0,04	1,069 ± 0,03	1,096 ± 0,04

For wildebeest, correction factors of 1,2654; 1,3739 and 1,0496, determined for all large bodied animals in the May 1988, October 1988 and November 1989



for the limited data. were used in correcting density estimates for the significantly reduced visibility when looking into the sun on one side of the Sun Angle Correction Factors (Table 53). To adjust previous wildebeest density estimates, a mean correction factor of 1.1722 for large bodied animals Correction factors of 1.2077; 1.3788 and 1.1485 were also used in the May 1988, October 1988 and July 1989 density estimates of gemsbok because significant differences were found between the sunward and shaded side of north-south transects (Table 52). An overall significant difference ( $t=4.38$ ;  $df=55$ ;  $P<0.01$ ) between the two sides justified using a mean correction factor of 1.1838 for gemsbok in previous censuses for which no correction factors were determined.

500 m wide strips for both gemsbok ( $t=1.83$ ,  $df=4.0$ ,  $P<0.05$ ) and wildebeest (Table 52). The mean ( $\pm$ SD) number of gemsbok counted on the sunward and shaded side within 500 m strips along 14 transects in four aerial surveys undertaken in 1988 and 1989 in the KGNP.

Survey	Sun	Shaded	t-value
May 88	54,9 $\pm$ 31,1	82,4 $\pm$ 47,6	3,00; $P<0,01$
Oct 88	33,9 $\pm$ 26,1	75,1 $\pm$ 43,2	14,0; $P<0,01$
Jul 89	39,9 $\pm$ 22,2	53,9 $\pm$ 31,3	1,98; $P<0,05$
Nov 89	22,6 $\pm$ 17,4	31,9 $\pm$ 31,2	21,0; $P<0,05$

Table 53. The mean ( $\pm$ SD) number of large bodied animals (eland, gemsbok, wildebeest, red hartebeest and ostrich) counted on the sunward and shaded side within 500m strips along 14 transects in four aerial surveys undertaken in 1988 and 1989 in the KGNP.

Survey	Sun	Shaded	t-value
May 88	57,9 $\pm$ 32,4	99,8 $\pm$ 51,6	4,27; $P<0,01$
Oct 88	41,9 $\pm$ 26,3	92,0 $\pm$ 44,3	3,15; $P<0,01$
Jul 89	51,1 $\pm$ 21,8	61,8 $\pm$ 31,9	1,30; $P<0,05$
Nov 89	34,7 $\pm$ 19,1	60,8 $\pm$ 33,7	2,13; $P<0,05$

For wildebeest, correction factors of 1,2654; 1,3739 and 1,0496, determined for all large bodied animals in the May 1988, October 1988 and November 1989

censuses respectively, were used in correcting density estimates for the significantly reduced visibility when looking into the sun on one side of the transect on north-south transects (Table 53). To adjust previous wildebeest density estimates, a mean correction factor of 1.1722 for large bodied animals was used, owing to the overall difference between the sunward and shaded sides of the transects ( $t=4.03$ ;  $df=55$ ;  $P<0.01$ ).

### Population Estimates

The differences between the population estimates from corrected 300 m and 500 m wide strips for both gemsbok ( $t=1.83$ ;  $df=4.0$ ;  $P<0.05$ ) and wildebeest ( $t=2.05$ ;  $df=4.0$ ;  $P<0.05$ ) were not significant, although there was a tendency for the 300 m estimates to be slightly higher (Tables 54 & 55). Adjustment of population estimates derived from 500 m strip counts for both species resulted not only in larger estimates but smaller variations between surveys than for 300 m strip counts (Tables 54 & 55).

The gemsbok population was both larger and more stable in numbers than the wildebeest population. Gemsbok numbers increased with an average annual  $r_{max}$  of 0.071 between 1985 and 1988, but declined thereafter. Wildebeest numbers fluctuated widely with an average annual  $r_{max}$  of -0.229.

No significant differences were found between the line transect estimates of gemsbok density and those from corrected 300 m ( $t=0.09$ ;  $df=4.0$ ;  $P>0.05$ ) and 500 m ( $t=1.05$ ;  $df=4.0$ ;  $P>0.05$ ) strips transects, although the former method had generally higher estimates (Table 56). However, large differences ( $t=2.73$ ;  $df=4.0$ ;  $P<0.05$ ) existed between the line transect estimates and the uncorrected 500 m strip transect data.

From the October 1987 to November 1989 aerial surveys, it was estimated that 87.6% of all large species (eland, gemsbok, wildebeest, hartebeest and ostrich combined) sightings were within the 500 m strip. Using this approximate

Table 54. Estimated population sizes and densities ( $\text{km}^{-2}$ ) of gemsbok in the KGNP from 1985 to 1989 as determined from aerial surveys using 300 and 500 m wide strips. Estimates from corrected and uncorrected 500 m wide strips are also presented. CV= coefficient variation; 95 % = 95 % confidence limits.

Month/Year	STRIP WIDTH											
	300m (corrected)				500m (corrected)				500m (uncorrected)			
	Estimated Total	95 %	CV	Density	Estimated Total	95 %	CV	Density	Estimated Density	95 %	CV	Density
May 85					9514	1676	17,6	1,038	8080	2901	17,9	0,881
Sep 85					9733	1386	14,2	1,061	7259	2065	14,2	0,792
May 86					6648	1086	16,3	0,725	4950	1622	16,4	0,543
Oct 86					11574	2611	22,6	1,262	8065	3713	23,1	0,879
May 87					10278	1143	11,1	1,121	7648	1700	11,1	0,834
Oct 87	9316	1977	10,6	1,016	10181	671	6,6	1,110	7584	1001	6,6	0,827
May 88	13623	4164	15,3	1,486	12833	1350	10,6	1,399	9357	2008	10,7	1,020
Oct 88	14799	4380	14,8	1,614	12631	1493	11,8	1,377	8172	2218	13,6	0,891
Jul 89	12522	3087	12,3	1,366	8448	976	11,6	0,921	6776	1569	11,6	0,739
Nov 89	5818	1652	14,2	0,635	4529	561	12,6	0,494	4205	1046	12,4	0,459
Mean					9636				7205			
SE					817				1552			
CV					8,5				21,6			



Table 55. Estimated population total and densities (km<sup>2</sup>) of wildebeest in the KGNP from 1985 to 1989 aerial survey calculated using corrected 300 and 500m wide strips and uncorrected 500m strips. CV = coefficient of variation; 95 % = 95 confidence limits.

Month/Year	Strip Width											
	300m (corrected)				500m (corrected)				500m (uncorrected)			
	Estimated Total	95 %	CV	Density	Estimated Total	95 %	CV	Density	Estimated Total	95 %	CV	Density
MAY 85					875	822	47,0	0,095	754	703	46,4	0,082
SEP 85					5760	2559	22,2	0,628	4453	1976	22,2	0,486
MAY 86					515	620	60,2	0,056	396	475	59,9	0,043
OCT 86					336	509	75,9	0,037	248	390	78,6	0,027
MAY 87					431	768	89,1	0,470	336	596	89,3	0,037
OCT 87	2005	2226	55,5	0,219	1405	1312	46,7	0,153	1098	1025	46,6	0,120
MAY 88	493	493	50,1	0,054	302	291	48,3	0,033	207	202	48,8	0,023
OCT 88	373	691	93,0	0,041	381	476	62,5	0,042	258	323	62,4	0,028
JUL 89	19	25	67,7	0,002	11	15	65,2	0,001	11	15	136	0,001
NOV 89	1118	1319	58,9	0,122	688	781	56,8	0,075	615	679	56,8	0,067
MEAN					1070				837			
SE					584,7				1308			
CV					50,0				156,3			

proportion, in conjunction with mean perception and sun angle correction factors calculated in the same surveys, aerial survey results prior to 1985 (Mills, unpublished data) were adjusted to facilitate long term comparisons of the gemsbok and wildebeest populations (Appendix B). The long term mean population estimates of  $8088 \pm 2910$  ( $\pm$ SD) gemsbok had a notably small variation in comparison to the widely fluctuating wildebeest mean of  $4538 \pm 3826$  ( $\pm$ SD). The latter was greatly influenced by large immigrations in August 1979 and September 1985 and unrealistically low counts in July 1989. Removal of these extreme values from the wildebeest data set resulted in a more reasonable mean estimate of  $743 \pm 482$  ( $\pm$ SD) for the resident wildebeest population.

Table 56. Population estimates of gemsbok in the KGNP derived from the Fourier series line transect estimate during 1987-1989 aerial surveys. 95 % = 95 % confidence interval; CV = coefficients variation.

Month/ Year	Density ( $\text{km}^{-2}$ )	95 %	CV	Estimated Total	P
Oct 87	1,175	0,300	11,3	10775	P=0,054
May 88	1,566	0,359	10,3	14360	P=0,000
Oct 88	1,324	0,426	14,9	12141	P=0,000
Jul 89	1,624	0,438	12,5	14892	P=0,166
Nov 89	0,379	0,178	21,8	3475	P=0,000

From 1974 to 1989 gemsbok have shown a gradual increase in numbers with an annual  $r_{\text{max}}$  of  $0,061 \pm 0,247$  in comparison to the declining annual  $r_{\text{max}}$  of  $-0,104 \pm 0,676$  for wildebeest (excluding the extreme values).

### Ground Counts

The mean annual total counts of  $546 \pm 62$  ( $\pm$ SE) wildebeest along the Nossob and Auob rivers (in conjunction with data collected since 1973) was significantly (Wilcoxon matched pairs:  $T=24$ ;  $P<0,05$ ;  $n=16$ ) smaller and varied less than the corrected 500 m wide strip estimates from the aerial surveys (Tables 55 &



Table 57. Mean total counts of wildebeest along both the Auob and Nossob riverbeds from 1973 - 1978. CV=coefficient of variation; SE=standard error; n=number of counts.

Year	Mean	SE	CV	n
1973	461	62	13,5	5
1974	643	38	5,9	7
1975	671	70	10,4	10
1976	918	61	6,6	3
1977	765	42	5,5	8
1978	819	50	6,1	10
1979	1007	99	9,8	8
1980	778	108	13,9	9
1981	606	80	13,2	8
1982	421	34	8,1	10
1983	358	51	14,3	5
1984	414	80	19,3	10
1985	377	79	20,9	6
1986	159	37	23,3	4
1987	135	18	13,3	5
1988	322	81	25,2	4
1989	422	58	13,7	4
MEAN	546			
SE	62			
CV	11,4			
n	17			

57; Appendix B). The higher, less reliable aerial census estimate arises from the method of estimating total animal numbers by extrapolating an actual small number of seen animals to the whole park, which the wildebeest in fact do not use as they concentrate predominantly along the rivers (see Chapter 4). Thus, in the following analyses the wildebeest ground count data were used in preference to the aerial census data.

From the ground count data between 1974 and 1989, the wildebeest had a relatively larger, but still negative, rate of increase ( $r_{max}$ ) of  $-0,006 \pm 0,38$  than in comparison to that estimated from the aerial census data (see above).

### Population Estimates and Rainfall

Gemsbok population estimates (using the corrected 500 m strip data) were found to only correlate significantly with rainfall accumulated over the previous three years (Table 58), as described by the equation:

$y = 11788,1x^{-0,0009}$  ( $r=0,67$ ;  $n=15$ ;  $P<0,01$ ), where  $x$ =rainfall accumulated over the previous three years. While the wildebeest population estimates were noted to correlate with summer rainfall accumulated over the previous two ( $y=1630,2x^{-0,0023}$ ;  $r=0,52$ ;  $n=17$ ;  $P<0,05$ ) and three ( $y=1757,3x^{-0,0016}$ ;  $r=0,63$ ;  $n=17$ ;  $P<0,01$ ) years (Table 58).

Table 58. Correlation coefficients ( $r$ ) for the exponential relationships between wildebeest (using ground counts) and gemsbok (from aerial censuses) populations estimates and summer rainfall. Summer=summer rainfall for year; Prev. summer.=previous summer's rainfall; Accumulated 2 yr=summer rainfall accumulated summer rainfall of the previous two years; Accumulated 3yr=accumulated summer rainfall of the previous three years.

Species	Correlation Coefficients For Rainfall			
	Summer	Prev. Summer	Accumulated 2 yr	Accumulated 3 yr
Gemsbok	$r=0,36$ ; $n=15$ ; $P>0,05$	$r=0,43$ ; $n=15$ ; $P>0,05$	$r=0,50$ ; $n=15$ ; $P>0,05$	$r=0,67$ ; $n=15$ ; $P<0,01$
Wildebeest	$r=0,37$ ; $n=17$ ; $P>0,05$	$r=0,42$ ; $n=17$ ; $P>0,05$	$r=0,52$ ; $n=17$ ; $P<0,05$	$r=0,63$ ; $n=17$ ; $P<0,01$

Relationships between the rate of increase ( $r_{max}$ ) of the two species populations and different rainfall variables were best described by parabolic curves (Table 59). Wildebeest showed the strongest significant correlation with the summer rainfall of the year and that accumulated over the previous two years. The latter relationship is illustrated in Figure 41, and peaked at 575 mm of rainfall accumulated over the previous two years, well above the two year mean of 440

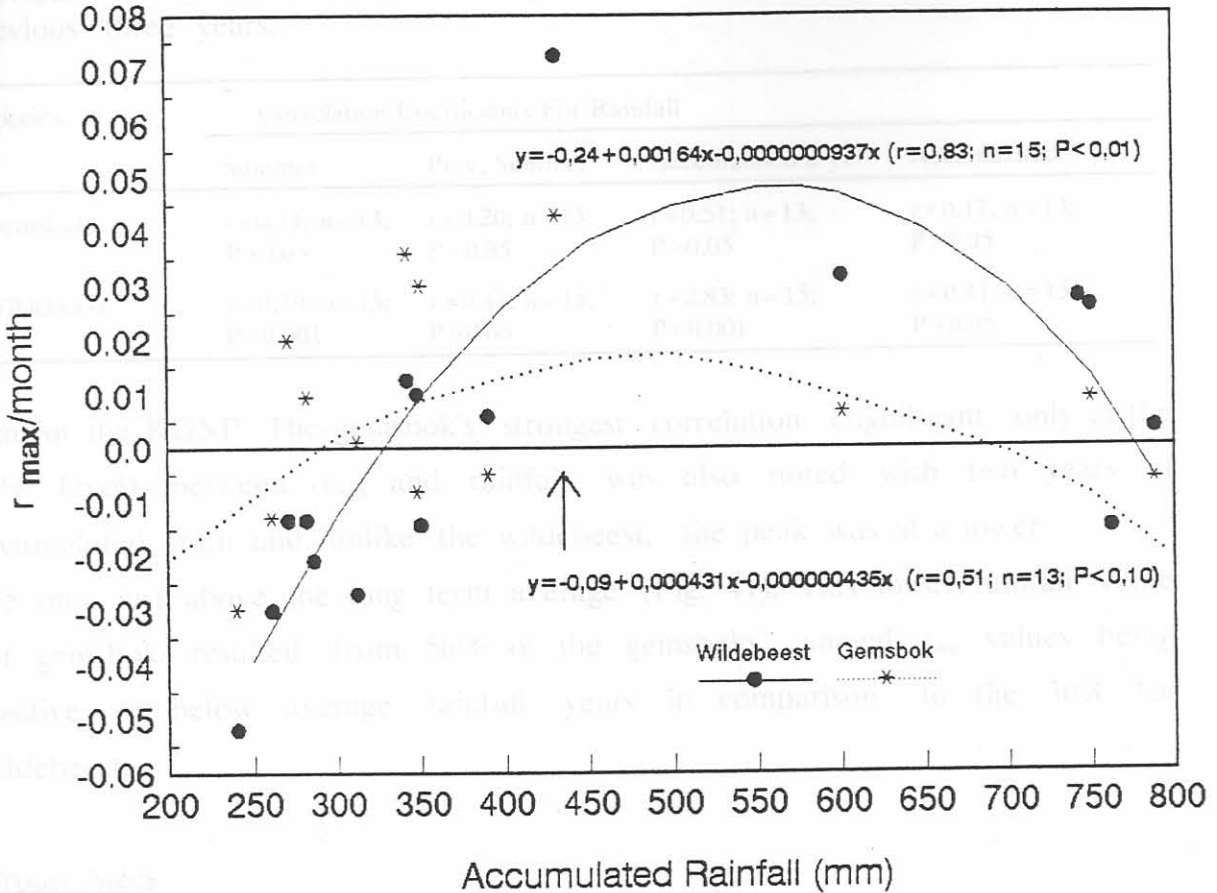


Fig. 41. The annual maximum rate of increase ( $r_{\max}$ ), corrected for month, for gemsbok and wildebeest against rainfall (mm) accumulated over two years. Arrow=long-term average rainfall for the KGNP.

Comparisons (with both groups lumped together) groups of wildebeest were in all cases greater (Wilcoxon matched pairs,  $T=0$ ,  $P=0.06$ ,  $N=5$ ) than those of gemsbok (Tables 60 & 61).

Comparisons with log transformed rainfall variables of summer rainfall and the accumulated rainfall of the previous 6, 12, 24 and 36 months revealed only a single significant correlation ( $y=2.639+0.522x$ ;  $r=0.43$ ;  $n=33$ ;  $P=0.012$  where  $x=\log$  of rainfall) between the logged typical group size of gemsbok males and rainfall accumulated over 36 months.



Table 59. Correlation coefficients ( $r$ ) for the parabolic relationships between wildebeest (using ground counts) and gemsbok (from aerial censuses) annual rates of increase ( $r_{max}$ ), corrected by month, against summer rainfall. Summer=summer rainfall for year; Prev. summer.=previous summer's rainfall; Accumulated 2 yr=summer rainfall accumulated summer rainfall of the previous two years; Accumulated 3yr=accumulated summer rainfall of the previous three years.

Species	Correlation Coefficients For Rainfall			
	Summer	Prev. Summer	Accumulated 2 yr	Accumulated 3 yr
Gemsbok	$r=0.31; n=13;$ $P>0,05$	$r=0.20; n=13;$ $P>0,05$	$r=0.51; n=13;$ $P>0,05$	$r=0.17; n=13;$ $P>0,05$
Wildebeest	$r=0.79; n=15;$ $P<0,001$	$r=0.41; n=15;$ $P>0,05$	$r=0.83; n=15;$ $P<0,001$	$r=0.41; n=15;$ $P>0,05$

mm for the KGNP. The gemsbok's strongest correlation (significant only at the 10% level) between  $r_{max}$  and rainfall was also noted with two years of accumulated rain and, unlike the wildebeest, the peak was at a lower 475 mm, just above the long term average (Fig. 41). This lower rainfall value for gemsbok resulted from 56% of the gemsboks' annual  $r_{max}$  values being positive in below average rainfall years in comparison to the 30% for wildebeest.

### Group Sizes

All group size variables increased ( $P<0,05$ ) with increasing total numbers of animals counted for both gemsbok and wildebeest. Adult female, male and combined (both groups lumped together) groups of wildebeest were in all cases greater (Wilcoxon matched pairs;  $T=0; P=0,03; N=5$ ) than those of gemsbok (Tables 60 & 61).

Comparisons with log transformed rainfall variables of summer rainfall and the accumulated rainfall of the previous 6, 12, 24 and 36 months revealed only a single significant correlation ( $y=2,639+0,522x; r=0,43; n=33; P=0,012$  where  $x=\log$  of rainfall) between the logged typical group size of gemsbok males and rainfall accumulated over 36 months.

Table 60. Mean (MEAN) and typical (TYP) group size of combined gemsbok, predominantly female, and male groups for each year from 1984 to 1989 in the KGNP.

YEAR	Combined					Female					Bull				
	MEAN	SD	TYP	SD	N	MEAN	SD	TYP	SD	N	MEAN	SD	TYP	SD	N
1984	4,36	3,3	14,16	9,5	531	7,34	4,9	15,90	7,5	202	1,08	0,1	1,23	0,3	282
1985	4,32	9,9	17,08	23,9	501	7,44	2,3	19,64	20,3	212	1,13	0,1	1,29	0,3	277
1986	4,01	6,0	16,05	22,2	227	7,93	10,6	19,14	18,0	141	1,09	0,1	1,17	0,1	90
1987	5,14	4,5	15,01	22,7	253	8,09	5,4	16,52	10,6	114	1,04	0,1	1,09	0,2	139
1988	6,00	8,8	22,45	28,7	346	10,36	9,1	24,70	23,7	154	1,10	0,1	1,19	0,1	201
1989	5,13	3,2	19,71	16,7	385	8,51	5,8	20,40	12,5	164	1,13	0,1	1,13	0,1	203
MEAN	4,72	4,8	16,62	18,8	2243	8,11	6,5	18,76	15,5	987	1,10	0,1	1,24	0,3	1192

Table 61. Mean (MEAN) and typical (TYP) group sizes of combined wildebeest, female and bachelor groups for each year from 1984 to 1989 in the KGNP.

Year	Combined					Female					Bull				
	MEAN	SD	TYP	SD	N	MEAN	SD	TYP	SD	N	MEAN	SD	TYP	SD	N
1984	9,33	18,8	47,96	41,4	324	34,71	26,7	54,36	52,3	76	1,42	1,2	2,54	1,1	236
1985	10,4	18,3	56,95	53,1	250	23,95	23,5	47,63	37,8	106	1,49	1,2	2,55	1,3	144
1986	7,19	11,3	25,40	24,5	93	20,14	13,9	29,35	30,9	25	1,35	0,9	2,07	1,1	69
1987	8,52	13,9	30,60	12,6	91	22,56	16,7	34,54	15,8	31	1,24	0,7	1,67	0,4	60
1988	8,30	16,4	26,72	44,6	149	26,73	22,5	45,38	46,4	40	1,26	0,9	1,94	0,5	109
1989	12,8	22,2	51,63	14,1	154	31,50	29,5	57,22	16,1	53	1,98	2,5	4,96	4,2	101
MEAN	9,44	17,1	43,63	38,3	1061	27,57	22,8	46,11	40,9	331	1,45	1,2	2,58	1,9	719



On the other hand, wildebeest group sizes (log transformed) showed a greater response to rainfall (log transformed), with combined mean group sizes correlating negatively with the summer ( $y=1,18-0,11x$ ;  $r=-0,42$ ;  $n=32$ ;  $P=0,014$ ) and the previous 6 months rainfall ( $y=2,45-0,07x$ ;  $r=-0,58$ ;  $n=32$ ;  $P=0,0005$ ). This was similarly reflected by mean male group size, but not the mean female group size which showed a significantly positive correlation with the previous 12 months rainfall ( $y=1,73+0,35x$ ;  $r=0,36$ ;  $n=32$ ;  $P=0,038$ ). Mean group sizes of wildebeest males correlated positively with summer rainfall ( $y=0,745-4,038x$ ;  $r=-0,44$ ;  $n=32$ ;  $P=0,01$ ), the previous 6 months of accumulated rainfall ( $y=2,032-1,677x$ ;  $r=-0,40$ ;  $n=32$ ;  $P=0,02$ ) and, like the gemsbok males, with rainfall accumulated over the previous 36 months ( $y=2,64+0,256x$ ;  $r=0,35$ ;  $n=33$ ;  $P<0,045$ ).

Although both the mean and typical group size data for the combined and female wildebeest categories showed a decline in 1986, a year after the large die-off, no significant differences between years for any of the categories were found. Gemsbok data also showed a lack of significance between years for combined, mixed and male group categories.

Comparisons of group size data for both species by seasons (subdivided into either broad summer and winter, and finer hot-dry, hot-wet and cold-dry periods) failed to produce any significant differences, probably arising from the wide standard deviations associated with the data.

Comparisons of the combined group class frequencies for gemsbok revealed significant differences between years ( $\chi^2=90,7$ ;  $df=30$ ;  $P=0,00$ ) (Table 62). With the advent of higher rainfall in 1988 and 1989, appreciable increases in the frequency of larger group sizes occurred.

No significant differences between the combined gemsbok group frequencies for summer and winter seasons ( $\chi^2=5,91$ ;  $df=6$ ;  $P=0,433$ ) were found, but the further subdivision into hot-dry, hot-wet and cold-dry seasons, revealed

Table 62. Percentage frequencies of combined gemsbok group size classes between 1984-1989.

Year	Group Size Class							n
	1	2 - 5	6 - 10	11 - 20	21 - 30	31 - 40	>40	
1984	6.5	26.8	14.8	12.1	5.8	2.8	1.41	531
1985	37.1	25.5	16.7	11.9	4.8	2.0	2.40	501
1986	40.2	26.9	13.3	4.8	6.7	5.2	2.9	227
1987	35.6	25.9	12.8	14.1	5.9	2.8	2.8	253
1988	33.7	23.1	15.1	11.6	5.0	5.9	5.3	346
1989	31.8	25.4	14.1	12.0	7.0	5.8	4.1	385

Table 63. Percentage frequencies of combined gemsbok group size classes for the hot-dry (HD), hot-wet (HW) and cold-dry (CD) seasons.

Season	Group Size Class							N
	1	2-5	6-10	11-20	21-30	31-40	>40	
HD	38.3	27.2	14.1	9.5	6.4	4.7	2.1	707
HW	35.2	24.3	14.0	13.5	5.7	5.0	4.0	559
CD	35.1	25.3	16.1	12.8	5.4	3.6	3.0	1066

significant differences ( $\chi^2=29.2$ ;  $df=12$ ;  $P=0.004$ ) between the three seasons (Table 63). The cold-dry and particularly hot-wet seasons appeared to have a greater preponderance of larger groups than the hot-dry period.

Wildebeest group size frequencies for male ( $\chi^2=159$ ;  $df=15$ ;  $P=0.0001$ ) and female ( $\chi^2=635$ ;  $df=25$ ;  $P=0.0001$ ) groups differed significantly between years (Table 64). Fewer larger groups of females occurred in 1986 and 1987, the two years after the 1985 die-off, while fewer larger male groups occurred only in 1987.

Comparisons of the sex and age compositions between the two species revealed notably more ( $\chi^2=209$ ;  $df=38$ ;  $P=0.001$ ) males within the gemsbok than wildebeest population, while more yearlings and calves amongst the latter species (Figs 42 & 43).

Table 64. Percentage frequencies of wildebeest female and male group size classes between 1984-1989.

Sex	Year	Group Size Class				N
		1	2-5	6-10	>11	
Males	1984	74,1	19,1	5,7	1,2	236
	1985	70,6	23,2	6,1	0,0	144
	1986	74,1	19,4	6,5	0,0	69
	1987	72,6	17,4	0,0	0,0	60
	1988	81,3	14,7	4,0	0,0	109
	1989	70,6	16,8	6,1	6,5	101

Sex	Year	Group Size Class							N
		1	2-5	6-10	11-20	21-30	31-40	>40	
Females	1984	2,5	8,6	15,3	13,5	13,3	10,1	36,8	76
	1985	0,9	17,3	16,7	21,0	12,4	5,6	26,4	106
	1986	--	19,7	13,2	22,6	13,4	16,9	14,0	25
	1987	3,2	20,0	14,4	7,3	26,3	21,6	7,3	31
	1988	--	3,1	23,4	30,0	17,2	4,4	21,6	40
	1989	--	12,6	7,8	14,3	25,8	11,6	27,9	53

Both female ( $\chi^2=57,9$ ;  $df=5$ ;  $P=0,0001$ ) and male ( $\chi^2=69,6$ ;  $df=3$ ;  $P=0,0001$ ) wildebeest group class frequencies differed significantly between summer and winter, with a shift towards less larger groups in summer than winter for both sexes. This was particularly noticeable for females in the hot-dry period and for the males in the hot-wet period of the summer months (Table 65).

#### Group Composition and Sex Ratios

Comparisons of the sex and age compositions between the two species revealed notably more ( $\chi^2=200$ ;  $df=381$ ;  $P=0,001$ ) males within the gemsbok than wildebeest population, while more yearlings and calves amongst the latter species (Figs 42 & 43).



Table 65. Percentage frequencies of wildebeest female and male group size classes between the hot-dry (HD), hot-wet (HW) and cold-dry seasons (CD).

Sex	Season	Group Size Class				N
		1	2-5	6-10	>11	
Males	HD	76,8	20,6	0,0	2,5	167
	HW	81,7	13,9	4,5	0,0	292
	CD	68,2	21,5	9,4	0,9	260

Sex	Season	Group Size Class						N	
		1	2-5	6-10	11-20	21-30	31-40		>41
Females	HD	--	13,9	16,9	22,3	15,6	10,3	20,9	103
	HW	--	17,4	8,8	16,1	18,5	10,8	28,3	97
	CD	--	12,1	18,5	13,4	18,0	11,9	26,1	135

Yearly comparisons showed significantly larger proportions of adult male ( $F=3,49$ ;  $df=5,0$ ;  $P=0,017$ ) and female gemsbok ( $F=2,77$ ;  $df=5$ ;  $P=0,002$ ) in 1986 and 1988 respectively (Fig. 42). Although the calf percentage declined in 1986, a year after the drought in 1985, the difference was not significant ( $F=2,3$ ;  $df=5$ ;  $P=0,078$ ).

The incorporation of wildebeest data collected prior to 1984 (Mills, unpublished data) revealed yearly variations in adult male ( $F=2,82$ ;  $df=11$ ;  $P=0,005$ ), yearling ( $F=11,5$ ;  $df=11$ ;  $P=0,001$ ) and calf ( $F=4,79$ ;  $df=11$ ;  $P=0,0001$ )

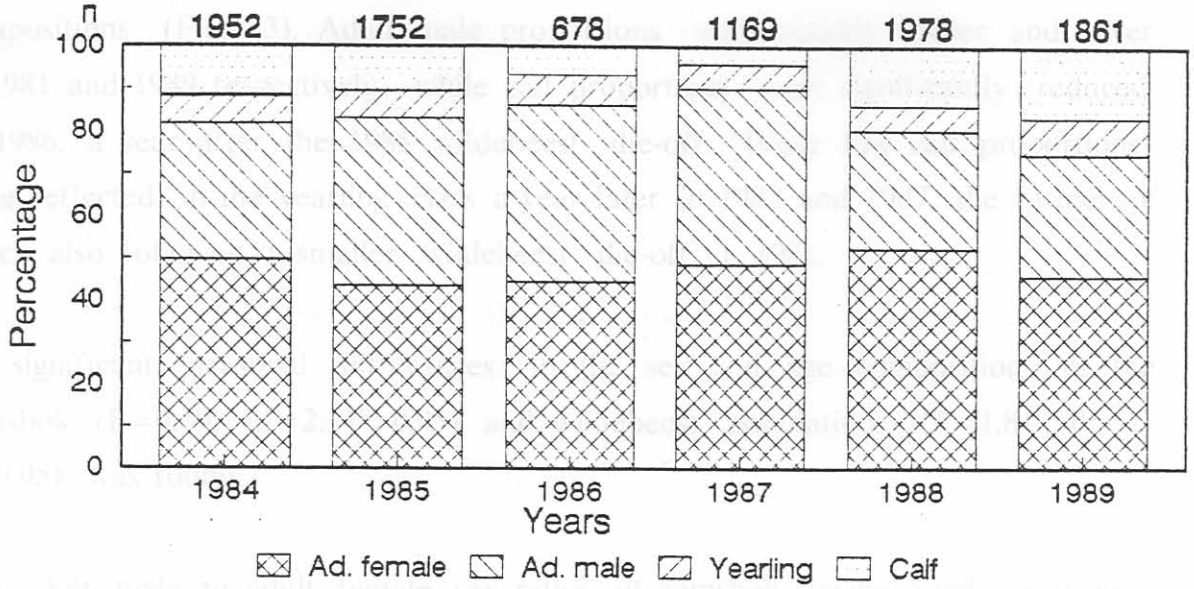


Fig. 42. The sex and age composition (%) of the gemsbok population in the KGNP from 1984-1989.

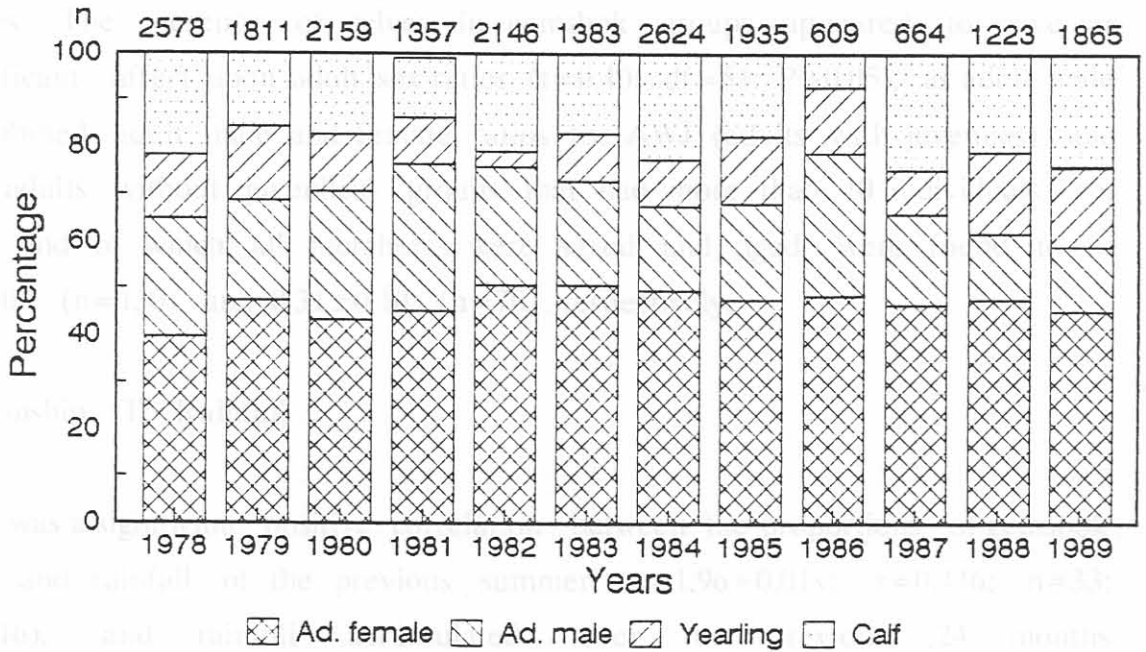


Fig. 43. The sex and age composition (%) of the wildebeest population in the KGNP from 1978-1989.

compositions (Fig. 43). Adult male proportions were notably higher and lower in 1981 and 1989 respectively, while calf proportions were significantly reduced in 1986, a year after the 1985 wildebeest die-off. These low calf proportions were reflected in the yearling class a year later in 1982 and 1987, the former of which also followed a smaller wildebeest die-off in 1981.

As with the group size data, wildebeest sex and age compositions showed. No significant seasonal differences in the sex and age composition of the gemsbok ( $F=0,19$ ;  $df=2$ ;  $P>0,05$ ) and wildebeest populations ( $F=1,84$ ;  $df=2$ ;  $P>0,05$ ) was found.

The adult male to adult female sex ratios of gemsbok (using road count data between 1984-1989) averaged one male to  $1,39 \pm 0,39$  ( $\pm SD$ ) ( $n=33$ ) females, while the wildebeest ratio averaged one male to  $2,78 \pm 2,23$  ( $\pm SD$ ) ( $n=33$ ) females. The presence of calves in gemsbok groups appeared to have an insignificant affect upon adult sex ratios ( $t=0,40$ ;  $df=51$ ;  $P>0,05$ ), as adult male to combined adult male and female ratios for AWJ (adults with juveniles) and ANJ (adults without juveniles) groups that had more than 10 individuals per group and of which all members were sexed and aged, were found to be  $0,9 \pm 0,08$  ( $n=130$ ) and  $0,31 \pm 0,10$  ( $n=70$ ) respectively.

#### Relationship To Rainfall

There was a significant positive correlation between the proportions of gemsbok calves and rainfall of the previous summer ( $y=1,96+0,01x$ ;  $r=0,416$ ;  $n=33$ ;  $P=0,016$ ), and rainfall accumulated over the previous 24 months ( $y=2,338+0,009x$ ;  $r=0,38$ ;  $n=33$ ;  $P=0,029$ ). No correlations between the proportion of adult females and accumulated rainfall were detected but a negative correlation between the proportion of adult males and the previous summers rainfall ( $y=2,79-0,016x$ ;  $r=-0,391$ ;  $n=33$ ;  $P=0,024$ ) existed.

Although, both the gemsbok and wildebeest adult male to adult female sex ratios, both wildebeest adult male to female ( $y=1,993+0,095x$ ;  $r=0,444$ ;  $P=0,010$ ;  $n=33$ ) and adult female to calf ( $y=0,28+0,003x$ ;  $r=0,38$ ;  $n=33$ ;  $P=0,029$ ) ratios were significantly correlated with accumulated rainfall over the previous 24 months. Adult gemsbok sex ratios did not correlate with any of the rainfall variables. But the adult female to calf ratios (which averaged one female to  $0,28 \pm 0,13$



calves (n=33) over the study period) however, correlated with the previous summer's rainfall ( $y=2,04+0,73x$ ;  $r=0,535$ ;  $n=33$ ;  $P=0,001$ ) and rainfall accumulated over the previous 24 months ( $y=2,38+0,52x$ ;  $r=0,524$ ;  $n=33$ ;  $P=0,002$ ).

As with the group size data, wildebeest sex and age compositions showed relatively stronger relationships with rainfall than gemsbok. Calf proportions correlated positively with the previous summer's rainfall ( $y=1,995+0,009x$ ;  $r=0,312$ ;  $n=80$ ;  $P=0,005$ ) and rainfall accumulated over the previous 24 months ( $y=2,41+0,006x$ ;  $r=0,231$ ;  $n=80$ ;  $P=0,039$ ). The proportion of yearlings also were found to correlate with the previous summer's rainfall ( $y=2,075+0,008x$ ;  $r=0,268$ ;  $n=80$ ;  $P=0,017$ ), rainfall accumulated over the previous 24 months ( $r=0,384$ ;  $P=0,004$ ;  $n=80$ ) and 36 months ( $y=2,55+0,01x$ ;  $r=0,354$ ;  $n=80$ ;  $P=0,001$ ) months. Amongst wildebeest adults, all correlations were found to correlate negatively with rainfall. The adult female proportions correlated negatively with the previous 24 months ( $y=2,99-0,01x$ ;  $r=-0,328$ ;  $n=80$ ;  $P=0,003$ ) and 36 months ( $y=3,21-0,01x$ ;  $r=-0,330$ ;  $n=80$ ;  $P=0,003$ ) of accumulated rainfall while the males showed a single correlation with the previous summer's rainfall ( $y=2,44-0,008x$ ;  $r=-0,328$ ;  $n=80$ ;  $P=0,003$ ).

With reference to the sex ratios, both wildebeest adult male to female (ie. one male to x number of females) ( $y=1,993+0,095x$ ;  $r=0,444$ ;  $P=0,010$ ;  $n=33$ ) and adult female to calf ( $y=2,016+0,53x$ ;  $r=0,463$ ;  $n=33$ ;  $P=0,007$ ) ratios showed positive correlations with the previous summer's rainfall. The increased adult male to female ratio in fact indicates an increase in female numbers relative to the males with increasing rainfall.

#### Relationship to Population Density.

Although, both the gemsbok and wildebeest adult male to adult female sex ratios (ie. one male to x number of females) showed positive and negative



trends respectively, with increasing population sizes, none of the relationships were significant (Figs 44 & 45).

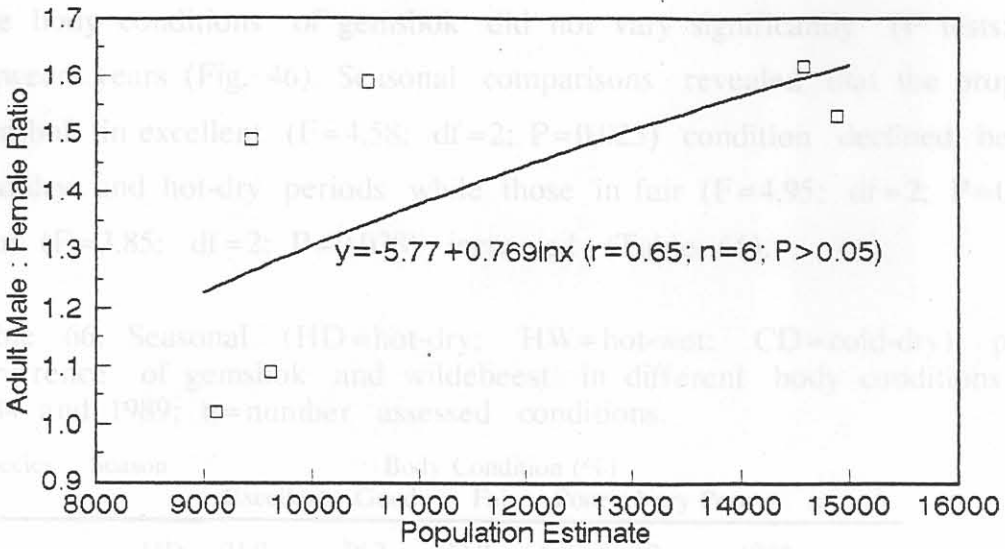


Fig 44. The mean annual gemsbok adult male to female (ie. one male to x number of females) against the annual population estimate.

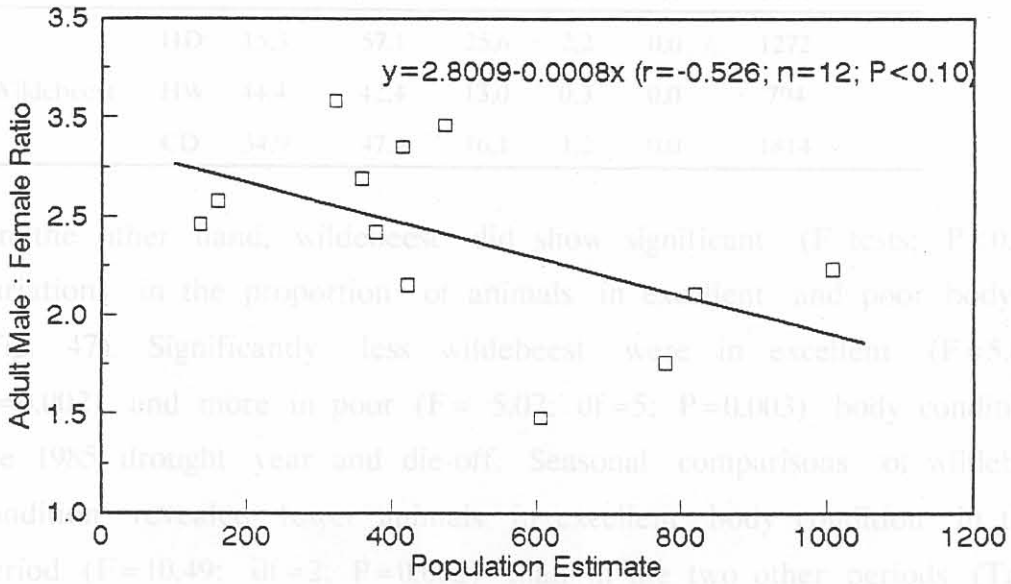


Fig 45. The mean annual wildebeest adult male to female (ie. one male to x number of females) against the annual population estimate.

### Body Conditions

The body conditions of gemsbok did not vary significantly (F tests:  $P > 0,05$ ) between years (Fig. 46). Seasonal comparisons revealed that the proportion of gemsbok in excellent (F=4,58; df=2;  $P=0,023$ ) condition declined between the cold-dry and hot-dry periods while those in fair (F=4,95; df=2;  $P=0,017$ ) and poor (F=3,85; df=2;  $P=0,038$ ) increased (Table 66).

Table 66. Seasonal (HD=hot-dry; HW=hot-wet; CD=cold-dry) percentage occurrence of gemsbok and wildebeest in different body conditions between 1984 and 1989; n=number assessed conditions.

Species	Season	Body Condition (%)					n
		Excellent	Good	Fair	Poor	Very Poor	
Gemsbok	HD	21,0	38,2	32,8	6,8	0,2	1730
	HW	45,4	39,7	19,8	3,1	0,1	1305
	CD	51,6	31,1	15,9	1,3	0,1	1974
Wildebeest	HD	15,3	57,1	25,6	2,2	0,0	1272
	HW	44,4	42,4	13,0	0,3	0,0	794
	CD	34,9	47,9	16,1	1,2	0,0	1814

On the other hand, wildebeest did show significant (F tests:  $P < 0,05$ ) yearly variations in the proportion of animals in excellent and poor body condition (Fig. 47). Significantly less wildebeest were in excellent (F=5,62; df=5;  $P=0,002$ ) and more in poor (F= 5,07; df=5;  $P=0,003$ ) body condition during the 1985 drought year and die-off. Seasonal comparisons of wildebeest body condition revealed fewer animals in excellent body condition in the hot-dry period (F=10,49; df=2;  $P=0,002$ ) than in the two other periods (Table 66).

For both gemsbok ( $y=0,91+0,02x$ ;  $r=0,563$ ;  $n=31$ ;  $P=0,001$ ) and wildebeest ( $y=1,09+0,02x$ ;  $r=0,636$ ;  $n=32$ ;  $P=0,001$ ) significant positive relationships existed between the proportion of animals in excellent body condition and accumulated rainfall over the previous six months.



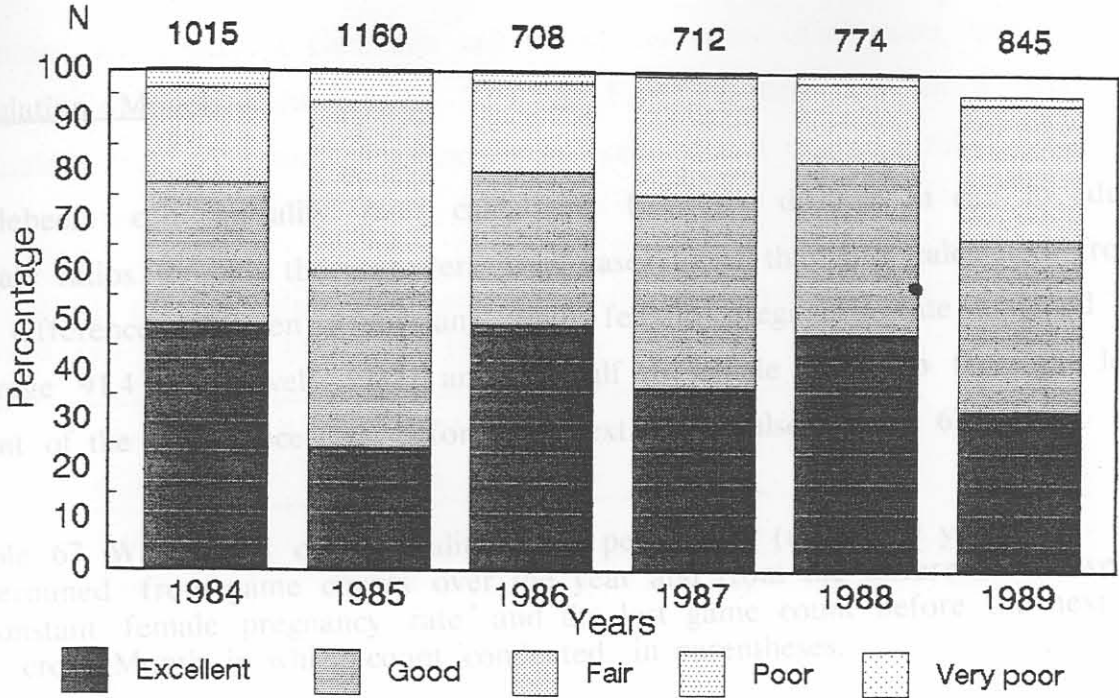


Fig. 46. The frequency (%) of gemsbok in different body conditions in each year from 1984-1989. N=number of animals assessed.

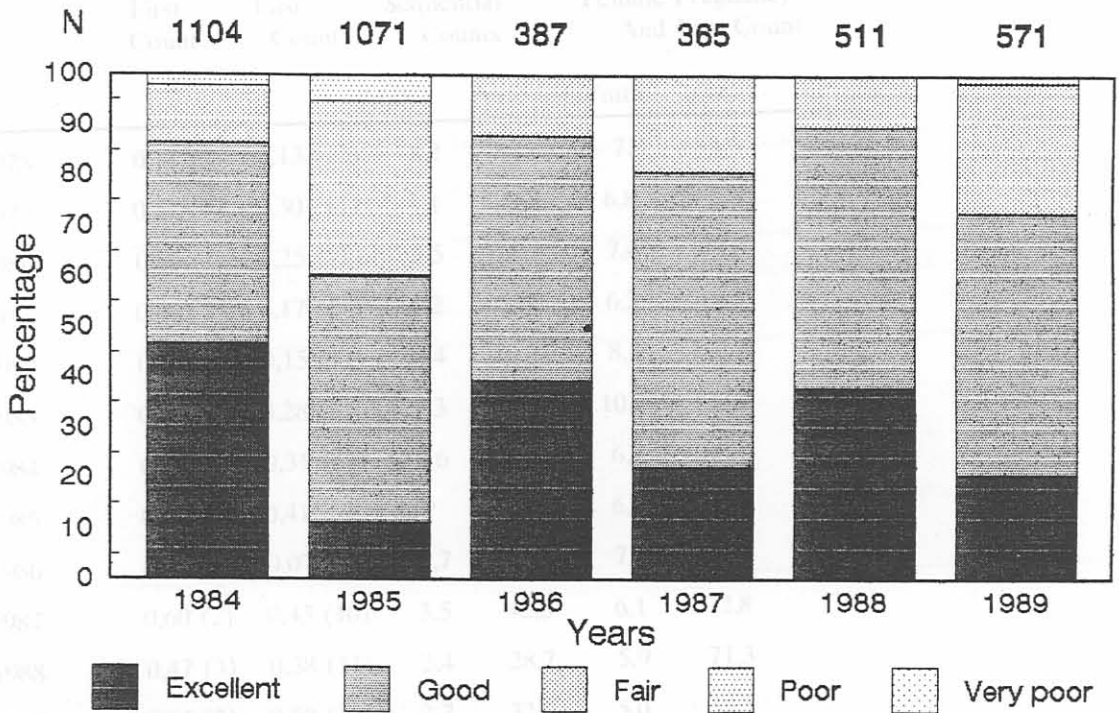


Fig. 47. The frequency (%) of wildebeest in different body conditions in each year from 1984-1989. N=number of animals assessed.

Gemsbok pregnancy rates for adult females were assumed to average 94.1 % as determined from 127 females shot in 1987 and 1988 in southern Namibia

(Mennie, pers comm'), Gemsbok calf mortalities were in all years significantly (matched pairs;  $T=0.00$ ;  $P<0.05$ ) than that for wildebeest. calculated from expected pregnancy percentages, and calf to female ratios of Wildebeest calf mortality rates calculated from the decline in calf to adult female ratios through the year were in all cases lower than that calculated from the difference between a constant adult female pregnancy rate assumed to average 91.4 % (Attwell 1982) and the calf to female sex ratio from the last count of the year concerned before the next birth pulse (Table 67).

Table 67. Wildebeest calf mortality rates per month (mth) and year (yr) determined from game counts over the year and from the difference between a constant female pregnancy rate\* and the last game count before the next calf crop. Month in which count conducted in parentheses.

Year	Calf : Adult Female			Calf Mortality (%)		
	First Count	Last Count	Sequential Counts	Female Pregnancy And Last Count		
			/mth	/yr	/mth	/yr
1978	0.71 (2)	0.13 (12)	8.2	98.0	7.8	94.6
1979	0.51 (1)	0.30 (11)	4.1	49.4	6.8	82.0
1980	0.56 (1)	0.25 (11)	5.5	66.4	7.4	88.8
1981	0.36 (1)	0.17 (11)	5.2	52.8	6.2	74.5
1982	0.62 (2)	0.15 (11)	8.4	101.1	8.5	102.0
1983	0.44 (3)	0.28 (8)	7.3	87.2	10.6	127.0
1984	0.53 (1)	0.31 (11)	4.6	55.2	6.7	80.7
1985	0.32 (3)	0.41 (9)	?	?	6.6	105.8
1986	0.23 (3)	0.07 (12)	7.7	92.8	7.0	84.5
1987	0.60 (2)	0.43 (10)	3.5	42.5	6.1	72.8
1988	0.47 (3)	0.38 (11)	2.4	28.7	5.9	71.3
1989	0.64 (2)	0.50 (10)	2.7	32.0	5.0	59.5
MEAN			5.4	64.3	7.1	87.0

\* Pregnancy rate assumed at 91.4 % (Attwell 1982).

Gemsbok pregnancy rates for adult females were assumed to average 94.1 %, as determined from 127 females shot in 1987 and 1988 in southern Namibia



(Mennie, pers comms <sup>1</sup>). Gemsbok calf mortalities were in all years significantly lower (Wilcoxon matched pairs;  $T=0,00$ ;  $P<0,05$ ) than that for wildebeest, calculated from expected pregnancy percentages, and calf to female ratios of the last count (Table 68).

Table 68. Gemsbok calf mortality rates per month (mth) and year(yr) determined for the differences between a constant female pregnancy rate\* and average calf : female ratios per year.

Year	Mean Calf:Female Ratio	Calf Mortality (%)	
		% Mth	% Yr
1984	0,22 ± 0,12	6,3	76,4
1985	0,29 ± 0,11	5,8	69,2
1986	0,16 ± 0,04	6,9	83,2
1987	0,28 ± 0,11	5,8	70,0
1988	0,41 ± 0,14	4,7	56,7
1989	0,42 ± 0,08	4,6	55,0
MEAN		5,7	68,4

\* Pregnancy rate assumed at 94,1% (Mennie, pers comms)

Table 69. Adult gemsbok and wildebeest survival rates. n= number of collared animals.

Species	Male	Sex n	Female	Test n	Combined Sexes	Test
Gemsbok	0,750	32	0,758	33	U = 12; N = 5 & 7; P = 0,50	0,717
Wildebeest	0,615	13	0,652	23	U = 10; N = 5 & 5 P = 0,143	U = 3; N = 5 & 5; P = 0,028

Adult survival rates, estimated from the survival of radio-collared animals, did not differ significantly between the sexes for both gemsbok ( $U=12$ ;  $n=5$  &  $5$ ;  $P=0,50$ ) and wildebeest ( $U=10$ ;  $n=5$  &  $5$ ;  $P=0,143$ ), although in both cases female survival rates slightly exceeded those of males (Table 69). Combined survival rates of gemsbok were greater ( $U=3$ ;  $n=5$  &  $5$ ;  $P=0,028$ ) than

<sup>1</sup> Mr. G. Mennie, PO Box 22, Koës, Namibia.

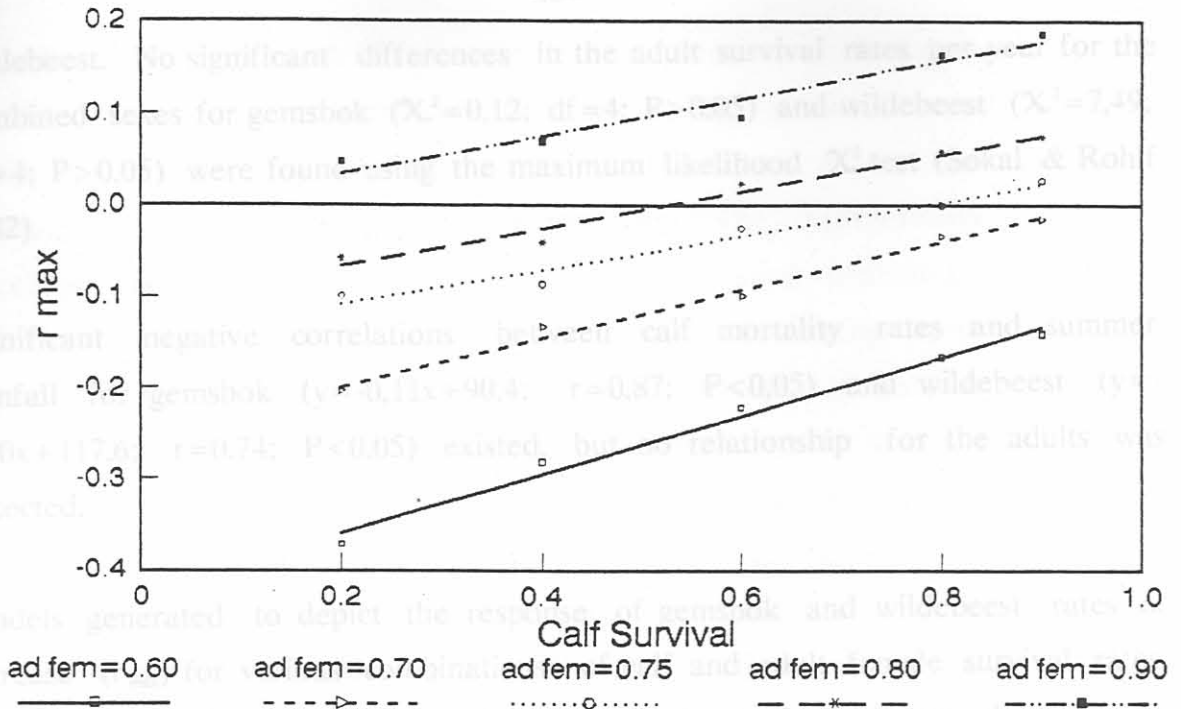


Fig. 48. Expected exponential rates of increase ( $r_{max}$ ) of the gemsbok population with different calf and adult survival rates.

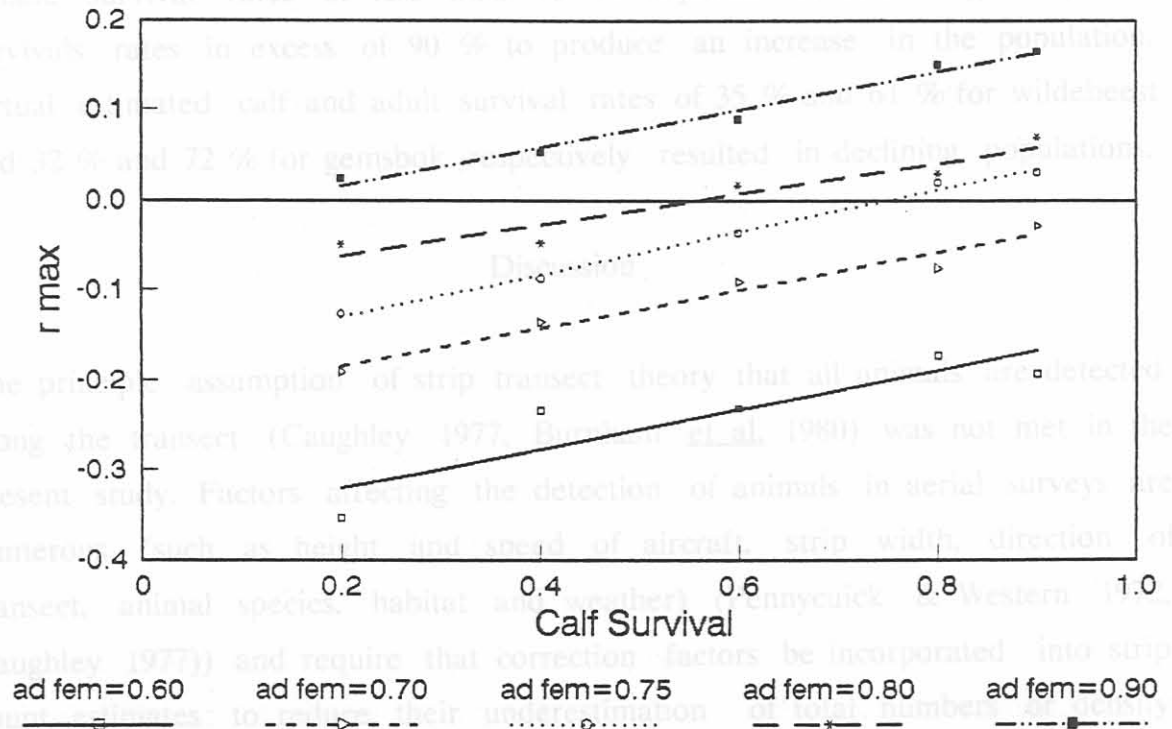


Fig. 49. Expected exponential rates of increase ( $r_{max}$ ) of the wildebeest population with different calf and survival rates.

wildebeest. No significant differences in the adult survival rates per year for the combined sexes for gemsbok ( $\chi^2=0,12$ ;  $df=4$ ;  $P>0,05$ ) and wildebeest ( $\chi^2=7,49$ ;  $df=4$ ;  $P>0,05$ ) were found using the maximum likelihood  $\chi^2$  test (Sokal & Rohlf 1982).

Significant negative correlations between calf mortality rates and summer rainfall for gemsbok ( $y=-0,11x+90,4$ ;  $r=0,87$ ;  $P<0,05$ ) and wildebeest ( $y=-0,30x+117,6$ ;  $r=0,74$ ;  $P<0,05$ ) existed, but no relationship for the adults was detected.

Models generated to depict the response of gemsbok and wildebeest rates of increase ( $r_{max}$ ) for various combinations of calf and adult female survival rates with differing pregnancy rates for adult and yearlings (assumed to equal natality) showed similar response curves (Fig 48 & 49). For both species, adult female survival rates of less than 70 % required unrealistically high calf survival rates in excess of 90 % to produce an increase in the population. Actual estimated calf and adult survival rates of 35 % and 61 % for wildebeest and 32 % and 72 % for gemsbok respectively resulted in declining populations.

## Discussion

The principle assumption of strip transect theory that all animals are detected along the transect (Caughley 1977, Burnham *et al.* 1980) was not met in the present study. Factors affecting the detection of animals in aerial surveys are numerous (such as height and speed of aircraft, strip width, direction of transect, animal species, habitat and weather) (Pennycuik & Western 1972, Caughley 1977) and require that correction factors be incorporated into strip count estimates to reduce their underestimation of total numbers or density (Caughley & Grice 1982, Pollock & Kendall 1987).

Although, in the present study the perception correction factors did not differ significantly for the 100, 300 and 500 m strips, probably as a result of the



openness of the habitat, a trend of decreasing detection with distance from the aircraft was evident for gemsbok and large animal species lumped together. Similarly, the direction of the transects and position of the sun influenced counting efficiency and required adjustment. The incorporation of these correction factors into 500 m strips resulted in population estimates comparable with those calculated by the line transect method. Increasing strip width from 300 m to 500 m resulted in a play-off between decreased population estimates but increased accuracy (decreased CV's) that results from larger sample sizes (Hone 1988). The comparable CV's of the 300 and 500 m strips and line transect results suggested that the two strip widths may have fallen in the ideal range of widths in which the two methods had comparative accuracy in the habitat concerned (Burnham *et al.* 1980), or that the correction factors used in the strip method made the two methods more comparable. The line transect theory which employs estimates in determining the decreasing detection probability with distance (Burnham *et al.* 1980), requires as one of its principle tenets the detection of all animals along line zero. Assuming line zero to equal the first 100 m strip, revealed that all animals were not seen in the KGNP aerial surveys, as has been noted in other fixed-wing aerial surveys (Holt & Powers 1980 in Burnham *et al.* 1980) but not when using a helicopter (Hone 1988). This was however overcome by using a perception correction factor for the first 100 m to boost animal numbers counted in that strip, and in fact was the only correction factor necessary in this method. The method also uses a larger sample size owing to generally larger strips that can also effectively be unbounded. Use of both methods in estimating population numbers allows for greater flexibility and a means of counter checking the data.

Although the resident wildebeest population showed a catastrophic crash, it was The population densities and rates of increase of gemsbok and wildebeest showed different responses to rainfall. The exponential rate of increase ( $r_{max}$ ) of the gemsbok population peaked with an accumulated summer rainfall total of 475 mm (slightly above the long-term average rainfall of 440 mm), and below the 575 mm found for the resident wildebeest population. Furthermore, the presence of more positive  $r_{max}$  values for the gemsbok than wildebeest during the



below average rainfall years explains the positive and negative responses in the gemsbok and wildebeest populations respectively, to the drought conditions that prevailed from 1979 to 1987. It also elucidates differences in the distribution of both species. The gemsbok's distribution is centred in the more arid western regions of southern Africa that receive from 100-500 mm of rainfall annually while the wildebeest show a preference for the mesic savanna grasslands to the east that receive between 200-700 mm rainfall (Smithers 1983). Thus, the small resident wildebeest population in the KGNP are only maintained through the provision of drinking water (Mills & Retief 1984a, Knight *et al.* 1988).

The decline in the KGNP wildebeest population since 1979 probably resulted from a combination of a reduction in calf survival with decreasing rainfall, as was also noted in the Serengeti wildebeest population during below average rainfall years (Hilborn & Sinclair 1979), in addition to possibly lower conception and pregnancy rates as a result of poor body condition of the adult females reducing the percentage coming into oestrus and ovulating. The latter reasons may have accounted for the radical decline in the calf numbers in 1986 (Fig. 45), a year after a large die-off of wildebeest at the height of the drought (Knight, unpublished data). Sinclair (1977) found conceptions in adult female buffalo and wildebeest were influenced by their body condition at the time of conception. The large die-off of adults, and particularly females in 1985, would have further enhanced the population decline, as has also been found in other African ungulate populations that experience periodic die-offs (Sinclair 1979, Pellew 1983, Fryxell 1987a).

Although the resident wildebeest population showed a catastrophic crash, it was unfortunately not evident amongst the collared animals from which estimates of adult mortality were determined, a reflection of possibly too small sample sizes (see Chapter 4). However, over the study period wildebeest adult mortality was estimated at a high 38.9% (reciprocal of survival (Table 69)), that exceeded both the 11% and 18% in the Serengeti (Sinclair 1979) and Zululand (Attwell 1982) populations respectively, and even the 10% found for other species such

as for the white-eared kob (Fryxell 1987b) and African buffalo (Sinclair 1974). Again this probably emanates from an inadequate sample size. On the other hand, the calf mortality estimated from sequential declines in the calf ratios ranged between 64% (assuming a constant natality of 91%) and 87%, and compares favourably with the 60-70% found in Zululand (Attwell 1982) and the 67% in the Serengeti (Hilborn & Sinclair 1979). Therefore, an estimated calf and adult mortality of 70% (survival=30%) and 38% (survival=62%) respectively, would have resulted in an incredibly large but negative  $r_{max}$  of -0.30 from the model, as illustrated in Figure 46. This was much larger than the estimated  $r_{max}$  of -0,01 from the ground census data. Assuming the calf mortality to be approximately correct, then the adult survival required to produce a  $r_{max} = -0,01$  would be about 85%, a more acceptable situation.

The drought prevailing from 1979 to 1987 appeared to have been advantageous to the resident gemsbok population. The population increase was probably attributable to an apparently lower adult mortality in combination with an overall lower calf mortality (68%) than found in wildebeest (87%), and particularly so at the lower rainfall regimes when gemsbok calf monthly mortality increased more gradually ( $y = -0,009x + 7,49$ ;  $r = 0,88$ ;  $n = 6$ ;  $P < 0,05$ ) than that of wildebeest ( $y = -0,012x + 9,0$ ;  $r = 0,51$ ;  $n = 12$ ;  $P < 0,10$ ). In addition, no catastrophic mortality occurred amongst the gemsbok during the 1985 drought (Knight, unpublished data), although a noticeable reduction in calf numbers occurred in 1985 and particularly in 1986 (Table 40), again possibly because of low conception rates owing to decreased body conditions recorded during that period (Table 44). Similar to the wildebeest, gemsbok adult mortality rates of 28,3% estimated from collared animals (Table 69) were high relative to those reported for other species (Sinclair 1974, Attwell 1982, Fryxell 1987a). An average calf mortality of 68% would have resulted in a population  $r_{max}$  of -0,15 from the model (Fig. 46), well below the estimated  $r_{max}$  of 0,06. Again assuming the adult mortality to be excessive, owing to inadequate small sample sizes, but a more accurate calf mortality, the adult survival rates required to produce a  $r_{max} = 0,06$  would be slightly above 90%, a distinctly possible situation.



Other population attributes such as age and sex composition, and group sizes also varied differently between gemsbok and wildebeest with respect to rainfall and population density. Both typical and mean group sizes of the combined and separate sexes of wildebeest were larger than gemsbok and probably stems from the fact that wildebeest being typical plains animals inherently form large groups (Leuthold 1977). Both species did however show considerable variation in group sizes indicative of not being particularly cohesive units, but possibly members of larger sub-associations, as also noted for fringe-eared oryx (Wacher 1986) and wildebeest (Attwell 1982). Estes (1966) however maintained that in the Ngorogoro crater groups were fairly stable for periods of up to five months, probably because of the large variations associated with the data. However, the mean and typical group sizes for gemsbok of five and 17 for combined groups (Table 60) from the southern Kalahari were smaller than the nine and 39 noted respectively on Galana ranch, Kenya (Wacher 1986). The large group sizes of the fringe-eared oryx population probably resulted from their higher densities of 1,4 individuals per km<sup>2</sup> in comparison to the 1,05/km<sup>2</sup> (n=10) from the KGNP that were maintained by a higher, more predictable rainfall in Galana. The increase in gemsbok population densities resulted in a concomitant increase in group sizes of gemsbok, but rainfall appeared to have no significant effect on group sizes except for a positive increase in male group size with rainfall accumulated over 36 months. The tendency to form larger groups in the wet season is probably in response to more abundant, widespread food supplies.

On the other hand, although the wildebeest population of the KGNP was relatively smaller than that in other large reserves in southern Africa, the average breeding herd group size of 28 was greater than the average of 12, 14 and 10 for the Kruger National Park (Mason 1986), Hluhluwe-Corridor-Umfolozi Game Reserve (Attwell 1982), and Ngorongoro crater (Estes 1969) respectively. But the KGNP's average bachelor herd size of 3,8 was smaller than the 6,5 and 5,6 noted in the Kruger National Park (Mason 1986) and Hluhluwe-Corridor-Umfolozi Game Reserve (Attwell 1982). Increases in animal densities resulted in further increases in group sizes of both breeding and bachelor herds. The larger breeding herd size in the KGNP appears initially to support the

hypothesis that group size increases with openness of the habitat (Leuthold 1977), however, the larger group sizes may in fact be in response to the attraction of the wildebeest to a few waterholes providing low-saline drinking water (Knight *et al.* 1988, see Chapter 6). The smaller bachelor herd size in the KGNP probably reflects the negative effect of increased aridity on herd size (Leuthold 1977), plus a possibly higher mortality rate amongst bachelors than adult males and females, as bachelor group size showed a stronger positive association with the previous 12 months rainfall than the breeding herds.

Gemsbok and wildebeest group sizes appeared relatively unaffected by seasons, probably because of the large variations associated with the data. However group size frequency distribution revealed larger mixed groups of gemsbok and breeding herds of wildebeest in the hot-wet period, similar to that noted for fringe-eared oryx (Wacher 1986), and wildebeest populations elsewhere (Talbot & Talbot 1963, Attwell 1982), and other ungulate species (Sinclair 1974, Jarman & Jarman 1974). However, the decline in wildebeest male group size in the hot-wet period coincides with their annual rutting period as also found by Attwell & Hanks (1980), while bachelor groups among gemsbok were rare.

None of the large fringe-eared oryx aggregations noted by Wacher (1986) were recorded for gemsbok in the KGNP. The tendency to form larger groups in the wet season is probably in response to more abundant, widespread food supplies and the added protection from predation granted by larger groups (Leuthold 1977).

The sex and age compositions of both species varied over the study period and appeared influenced by extrinsic (eg. rainfall) and intrinsic (eg. population density) factors. The percentages of calves and yearlings of both species were positively correlated with rainfall, while the proportion of gemsbok males, and both sexes of adult wildebeest declined with increasing rainfall. The positive relationship between rainfall and calf to adult female ratios for gemsbok and wildebeest ratified the above findings, and further suggests that calf survival is



indirectly dependent upon rainfall which directly stimulates the food source. Most non-violent mortalities are known to occur in the late dry season (Houston 1979). This period coincides with the time that wildebeest calves are weaned, which takes place at about eight months of age (Smithers 1983), and if the rainfall of the previous summer was below average, grazing is less abundant, providing conditions for increased mortality. In fact, more animals of both species were in poorer body condition during the hot-dry period (Figs 46 & 47), as similarly noted for wildebeest in Etosha National Park (Berry & Louw 1982a).

apparent shift in the sex ratio in response to extrinsic (rainfall) and intrinsic (population density) factors suggests the existence of a possible. Wacher (1986) reported that the presence of calves in mixed fringed-eared oryx herds appeared to have a negative influence on adult male numbers in the herds. This was not noted for gemsbok in the KGNP, which may indicate less active selection by lactating females to assemble together. Wacher (1986) noted that many fringe-eared oryx groups were frequently in sight of each other but this was not apparent in the KGNP, possibly because of the lower population densities in addition to the rolling dune habitat.

their varying breeding systems, social behaviour (Clutton-Brock, Guinness & Albon 1984) and feeding styles are. Amongst the wildebeest, the adult male to female sex ratios showed a similar positive correlation to rainfall ie. an increase in the female component with increasing rainfall. While the lack of correlation with the gemsbok's sex ratio may indicate that minimal stress was placed on the gemsbok population by the rainfall experienced or that their different social systems in which non-territorial males follow female herds and do not form separate bachelor herds restricted to suboptimal habitats as occurs with wildebeest (Estes 1969; Wacher 1986) was responsible. Declines in the adult wildebeest male component with increasing rainfall may have resulted from increased predation on these predominantly solitary individuals through better vegetational cover offered to stalk and pounce predators such as lion, their principle predator (Mills 1984).

The tendency (significant at 10% level) for increased males in the KGNP wildebeest population with increasing population sizes conforms with that found

for white-tailed deer (McCullough 1979). Verme (1965) inferred that the distortion of the sex ratio in favour of males arose from the females producing more males under stressful conditions, as occur at high population densities or in food shortages. Therefore for wildebeest, an apparent dichotomy appears to exist with the population size increasing following above average summer rainfall accumulated over three seasons (indicative of a delayed response), while adult male to female sex ratios increased positively with increasing rainfall of the previous summer but decreased with increasing population size. This apparent shift in the sex ratio in response to extrinsic (rainfall) and intrinsic (population density) factors suggests the existence of a possible negative feedback mechanism in the population regulation which may account for the parabolic response between the wildebeest populations rate of increase and rainfall. Furthermore, little can be drawn from the gemsbok's opposite insignificant trend in adult sex ratios to increasing density.

body size are considered one of the principle operative mechanisms (Jarman & The different responses in the two species densities, age and sex compositions and group sizes emphasises the extent to which their varying breeding systems, social behaviour (Clutton-Brock, Guinness & Albon 1984) and feeding styles are affected by the harsh southern Kalahari environment. the diverse physical and chemical properties characteristic of plants available to animals of different sizes and gut morphology (Owen-Smith 1982). For this reason the similar sized gemsbok and wildebeest, were chosen in the present study in order to reduce the problems associated with allometry and expose the other means of achieving resource partitioning by equivalent sized herbivores.

Owen-Smith (1985) considered muzzle width to be the second most important mechanism of resource partitioning, particularly amongst the grazers. The classical explanation that larger species utilize generally taller swards of more fibrous grasses because of a lower mass specific metabolism and longer retention times (Jarman 1974), may in fact be a misinterpretation (Illius & Gordon 1987). There is no reason to believe that they should not graze shorter, better quality grass communities unless compelled to. In the case of larger