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CHAPTER 4

MOVEMENT PATTERNS

Introduction

Movement patterns, range use, activity budgets and population dynamics exemplify the overall relation of a species to its environment and may alter with respect to habitat, season and even time of day. Africa, and more specifically the savanna ecosystems, home of the vast majority of ungulates, has many examples of different movement patterns amongst a range of species.

Although there are great difficulties in classifying the types of movement (Caughley 1977), Western (1975) recognised three categories of seasonal movement patterns : migratory, 'dispersal' and resident systems. He considered migration as a more regular long distance return movement between two areas which are largely, though not entirely, predictable in time and space, such as the migration of wildebeest (Pennycuick 1975), white-eared kob Kobus kob leucotis (Fryxell & Sinclair 1988b) and caribou Rangifer tarandus (Fancy, Pank, Whitten & Regelin 1989). 'Dispersal' movements referred to wet season dispersal and dry season concentrations and differed from migration in its more limited scale. Such dispersal movements also occur amongst wildebeest and zebra (Western 1975, Lamprey 1963, Whyte, pers comm. [1]). The resident system shows even more limited movements in both seasons, such as noted for the ungulates in the Ngorongoro crater and arid-adapted oryx, Oryx gazella beisa, Thompsons gazelle Gazelle thomsoni and gerenuk Litoeranius walleri in East Africa (Western 1975, Maddock 1979).

Migration and dispersal movements normally occur during transition periods between seasons (winter/summer or wet/dry periods) which suggests a response

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to seasonal changes in resource availability and/or quality (Fryxell & Sinclair 1988b). The ungulate migrations studied to date suggest that migration enables capitalization upon food patches of high quality and not the absolute abundance of food (Maddock 1979, Festa-Bianchet 1988, Fryxell, Greever & Sinclair 1988). The white-eared kob in the Boma National Park, Sudan and wildebeest in the Serengeti, Tanzania, both moved away from the high rainfall and more productive ranges in the wet season to areas with lower rainfall, reduced productivity but apparently better quality forages. The return to the higher rainfall regions takes place during the dry season in response to declining food quality and diminishing supplies of drinking water. The dependence upon drinking water plays an integral part in the dry season range selection by migrants and 'dispersers' alike, whereas the predominantly arid adapted 'resident' species, through physiological and behavioural characteristics, are able to survive independently of drinking water, and thus show little or no change in their movement patterns in the dry season (Western 1975).

Furthermore, it has been hypothesised that migration may have a selective advantage over the more resident movement patterns in that the migrants are possibly exposed to a lower risk of predation from territory bound predators. The advantages of exploiting temporary gluts of high quality food supplies and reduced predation risk through migratory behaviour may have worked in unison in shaping the migratory behavioural pattern (Fryxell, Greever & Sinclair 1988).

The central and southern Kalahari are also noted for their spectacular movements of ungulates, particularly by wildebeest, springbok and red hartebeest (Child & Le Riche 1969, Ngwamotsoko 1985, Williams, Williams & Ngwamotsoko 1988). The majority of mass movements which occur normally in drought years entailed periodic, dry season concentrations around lake Xau, and prior to the erection of the Khukhe veterinary cordon fence, the game also concentrated around Lake Ngami and along the Boteti river further to the north (Williamson & Williamson 1985). The direction of the wet season dispersion is predominantly to the south west, into the southern and central Kalahari where

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water is available for short periods in small pools in the scattered pans and from indigenous melon crops (Williams et al. 1988). In addition, it has been suggested that more infrequent dry season movements by wildebeest and other species, such as eland and red hartebeest, occurred in a possible attempt to reach the Orange river, far to the south (Williamson & Williamson 1986).

With the establishment of boreholes in the KGNP from the 1930's a small segment of the larger mobile wildebeest population stabilised in the park (Eloff 1966). Pressure of late from veterinary fences, stock farmers and hunters began to restrict the indigenous ungulates natural movements to within the KGNP-GNP-WMA, a conservation area amounting to 80 000 km^2 and covering about 40% of the southern Kalahari. Therefore, it was important to determine if the conservation area was sufficiently large enough to allow the natural movements of the large mammalian community. Hence, it was imperative to monitor the movements of individuals of the different species over a number of seasons. Specific attention was paid to wildebeest and gemsbok, as they are of comparable body mass and are grass and roughage feeders grazing predominantly grass (Hofmann & Stewart 1972), but differ with respect to their dependence upon drinking water. The wildebeest are considered to be obligate drinkers, while the gemsbok are one of the few grass and roughage feeders able to survive independently of drinking water (Taylor 1968, Western 1975). Thus in a semi-desert ecosystem with an average annual rainfall of 220 mm that comes in sporadic rainstorms, food quality is expected to be highly variable in time and space and with the recent provision of water, the gemsbok and newly resident wildebeest are expected to display different movement patterns and habitat use in relation to their feeding, water and mineral requirements.

Therefore the aim was to answer two questions: how large are individual ranges for each species by year, season and sex; and how the ranges varied in relation to habitats and their different qualities? The answers to these questions would also elucidate their differing requirements for water and the functional significance of foraging radii (Pennycuick 1979) in the Kalahari context.

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Home range was initially defined by Burt (1943) as that area transversed by the individual in the normal activities of food gathering, mating and caring for young and around which no time limit was set. Hence the term 'range' was used in conjunction with more descriptive terms such as annual, summer and winter.

Results

Accuracy of Locations

The actual and estimated positions of radio-collared animals were found not to differ significantly ($t=0,36$; $df=30$; $P>0,05$). As they averaged $1,9 \pm 0,5$ km ($\pm$SD) apart (with a 95 % confidence interval of 2,5 km), a grid cell size of 25 km^2 was used in the calculation of range sizes.

Population Ranges

None of the radio-collared gemsbok ($N=21$) wandered beyond the borders of the KGNP-GNP complex over the 1985-1989 study period (Figs 16 & 17). Only one of 19 radio-collared adult female wildebeests moved outside the KGNP-GNP borders in 1989 (Fig. 18). Comparisons of the total range used by adult females of both species revealed that the gemsbok were more catholic in their distribution in comparison to wildebeest, which concentrated predominantly along the Nossob and Auob riverbeds. The adult males of both species restricted their movements much more than the females (Figs 17 & 19).

Seasonal comparisons of the lumped distributional ranges of gemsbok females over the study period revealed an overall expansion towards the north east in the summer months and a contraction towards the west in the winter (Fig. 17). The gemsbok males failed to show such a pattern (Fig. 17). Wildebeest also did

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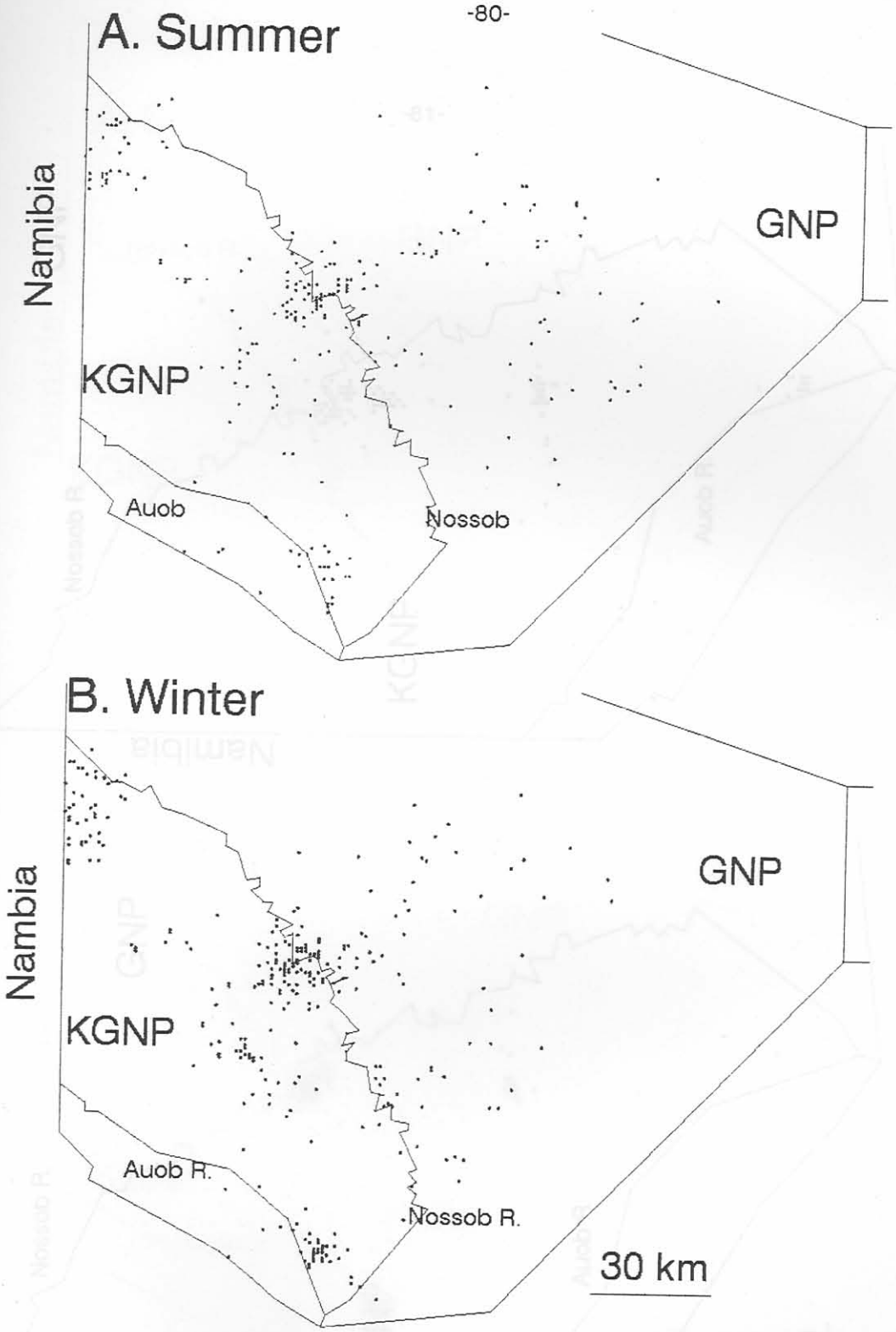

Fig 16. Locations of all radio-collared female gemsbok in the summer (A) (N=9, locations=237) and winter (B) (N=9, locations=245).

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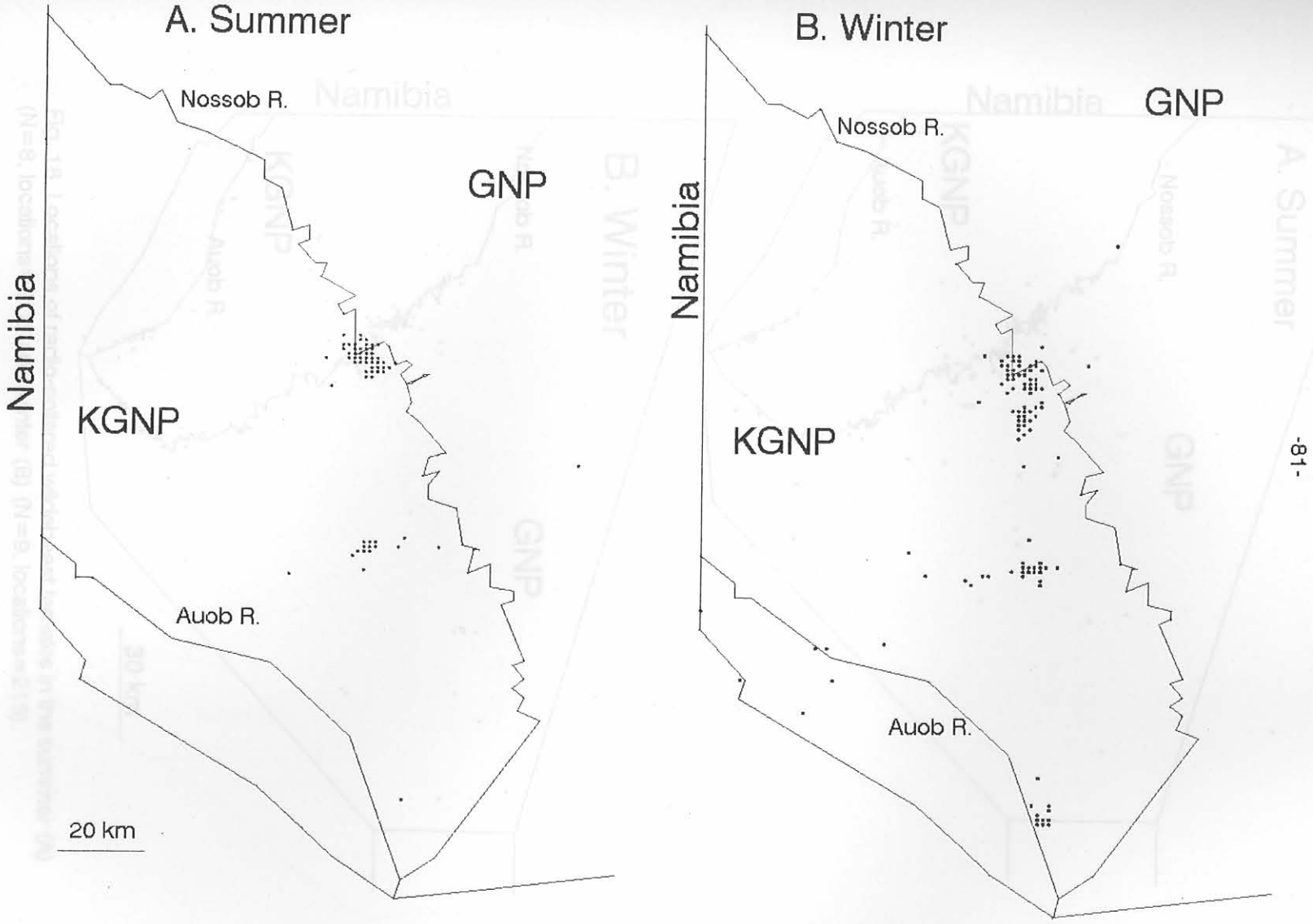

Fig 17. Locations of all radio-collared male gemsbok in the summer (A) (N=13, locations=178) and winter (B) (N=13, locations=245).

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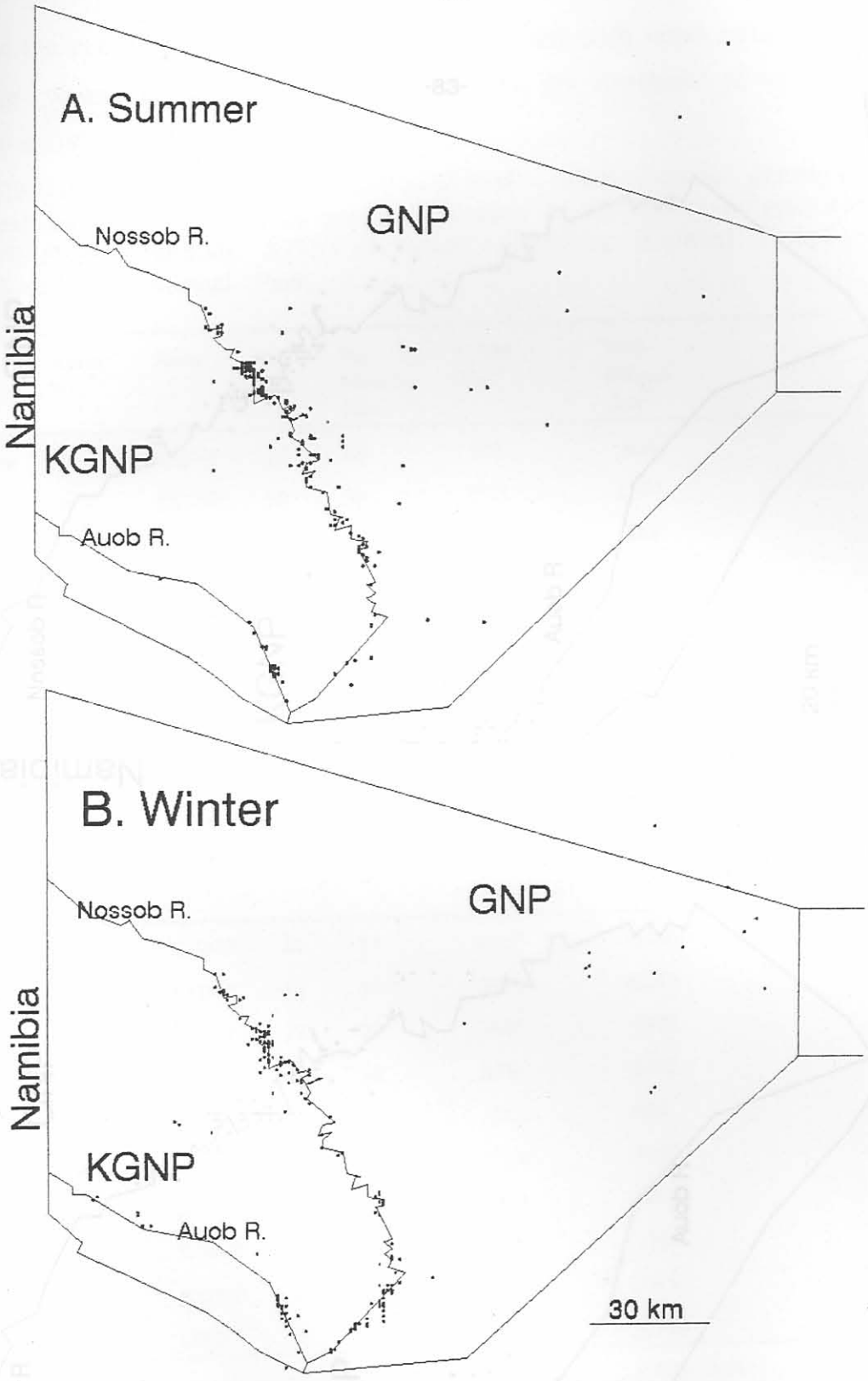

Fig. 18. Locations of radio-collared wildebeest females in the summer (A) (N=8, locations=212) and winter (B) (N=9, locations=213).

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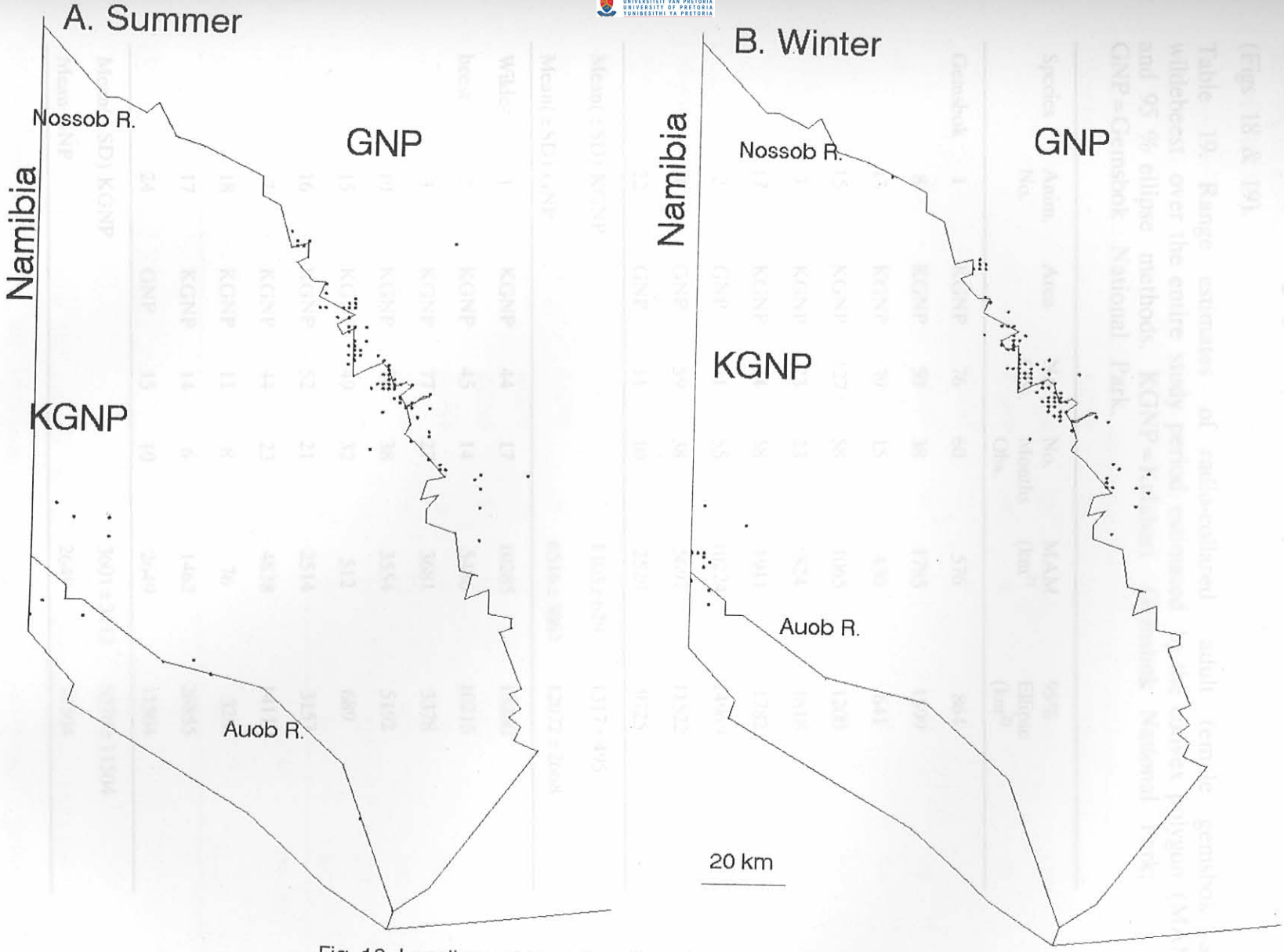

Fig. 19. Locations of all radio-collared wildebeest males in the summer (A) (N=9, locations=146) and winter (B) (N=7, locations=151).

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not show the gemsbok female range use pattern, but both sexes infrequently did undertake wider ranging movements away from the riverbeds in both seasons (Figs 18 & 19).

Table 19. Range estimates of radio-collared adult female gemsbok and wildebeest over the entire study period estimated by the convex polygon (MAM) and 95 % ellipse methods. KGNP=Kalahari Gemsbok National Park; GNP=Gemsbok National Park.

Species	Anim. No.	Area	No. Obs.	No. Months Obs.	MAM (km^2)	95% Ellipse (km^2)
Gemsbok	1	KGNP	76	60	576	864
	8	KGNP	50	38	1785	1599
	13	KGNP	39	15	430	641
	15	KGNP	127	58	1065	1200
	7	KGNP	23	23	824	1818
	17	KGNP	74	58	1941	1782
	2	GNP	71	55	10224	14969
	30	GNP	59	38	5697	11522
	22	GNP	11	10	2529	9725
Mean(±SD) KGNP					1103±629	1317±495
Mean(±SD) GNP					6516±3867	12072±2668
Wilde-	1	KGNP	44	17	10285	13280
beest	2	KGNP	45	14	5486	10215
	3	KGNP	77	27	3681	3378
	10	KGNP	70	38	3554	5192
	15	KGNP	49	32	512	689
	16	KGNP	52	21	2514	3157
	7	KGNP	44	23	4838	14110
	18	KGNP	11	8	76	328
	17	KGNP	14	6	1462	26855
	24	GNP	15	10	2649	11504
Mean(±SD) KGNP					3601±3112	8578±11504
Mean GNP					2649	11504

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Table 20. Range estminates of radio-collared adult male gemsbok and wildebeest over the entire study period estimated by the convex polygon (MAM) and 95 % ellipse methods. *=sub-adult and non-territorial. KGNP=Kalahari Gemsbok National Park; GNP= Gemsbok National Park.

Species	Anim. No.	Area	No. Obs.	No. Months Obs.	MAM (km^2)	95 % Ellipse (km^2)
Gemsbok	12	KGNP	19	23	67	145
	14	KGNP	58	35	120	123
	16	KGNP	80	36	46	53
	18	KGNP	11	7	2	11
	19	KGNP	47	22	73	90
	20	KGNP	83	21	32	26
	23	KGNP	42	22	71	146
	24	GNP	37	22	22	27
	25	GNP	36	22	21	26
	31*	GNP	35	19	3641	5024
Mean(±SD)KGNP					59±37	85±56
Mean GNP					22	27
Wild-	13	KGNP	123	46	353	223
beest	14	KGNP	12	10	2	27
	19	KGNP	29	11	403	627
	21	KGNP	22	13	1043	2658
	22	KGNP	4	4	22	111
	23	KGNP	30	13	423	710
	26	KGNP	32	12	93	158
	28	KGNP	11	3	78	267
Mean(±SD) KGNP					302±346	598±867
Mean GNP					-------	------

Development of Ranges with Time

Range estimates using the convex polygon or minimum area (MAM) and 95% ellipse methods for all locations for each radio-collared gemsbok and wildebeest are presented in Tables 19 & 20, respectively. For both gemsbok

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($t=2,16$; $df=8$; $P<0,05$) and wildebeest ($t=2,16$; $df=9$; $P<0,05$) females, the 95% ellipse estimates of home range were larger than those calculated by the MAM, while no differences between the two methods were detected for territorial males of both species. Thus, owing to the MAM's more conservative estimates of range use, greater flexibility of shape and more extensive use in the literature than the 95% ellipse method (White 1987), the former method was chosen for home range analyses.

Interspecific home range comparisons using MAM results revealed that both male ($t=2,72$; $df=12$; $P<0,05$) and female ($t=2,32$; $df=13$; $P<0,05$) wildebeest had larger ranges than the same sexes for gemsbok, although individual gemsbok were, on average, observed over significantly ($t=2,38$; $df=32$; $P<0,05$) longer periods. The non-territorial subadult gemsbok male no. 31 was excluded from the comparison.

Except for between female wildebeest MAM range estimates and the total number of days observed ($r_s=0,707$; $n=8$; $P<0,05$), no other significant relationships were found between home range estimates and the sampling variables of the number of observations and time period of observation. This lack of significant correlations probably arises from the non-linear response curves of the home range estimates with time. Gemsbok and wildebeest showed increasing home range sizes with accumulative sightings over time. Approximately 50% of the home range estimates of both gemsbok males, and females resident in the KGNP appeared to reach an asymptote after 20 - 25 sightings, while gemsbok females resident in the waterless GNP had continually increasing response curves, reaching larger home range sizes after the same number of locations (Figs 20 & 21). Home range estimates for 50% of wildebeest males and females also appeared to reach an asymptote between 20 - 30 sightings but their range sizes were larger than those of gemsbok for a similar number of locations (Figs 22 & 23). Thus satisfactory home range estimates per season and year were seldom reached and the estimates should rather be considered as indices of area use.

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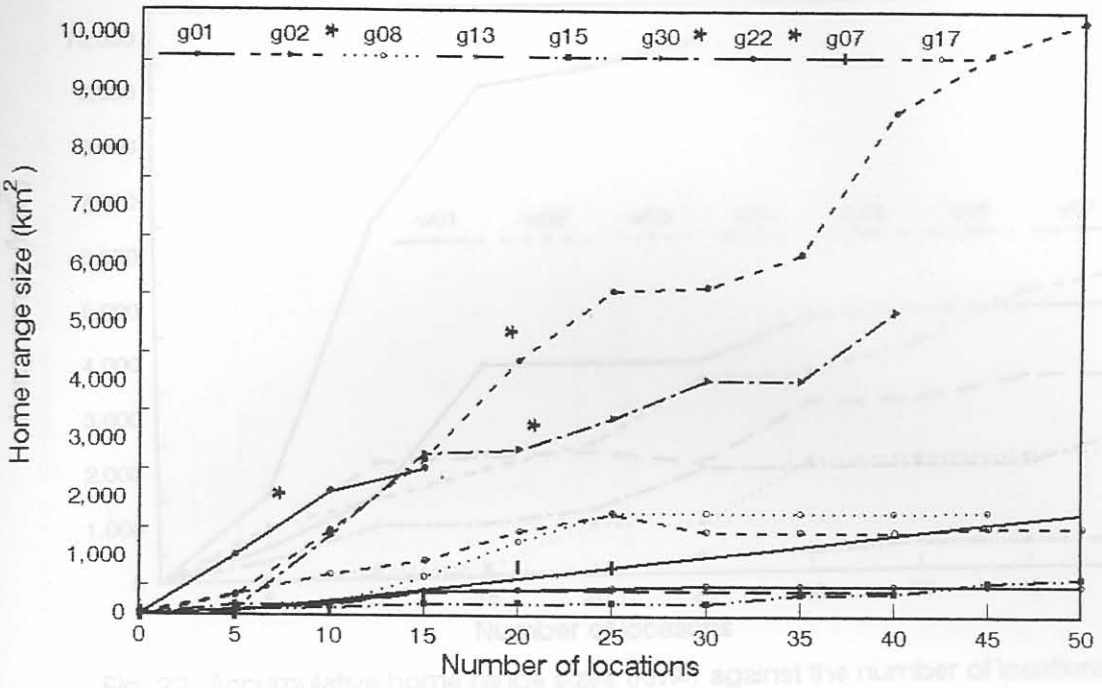

Fig. 20. Accumulative home range sizes (km2) against the number of locations for individual gemsbok females in the KGNP and GNP areas. Individuals with an '*' were resident in the GNP without drinking water.

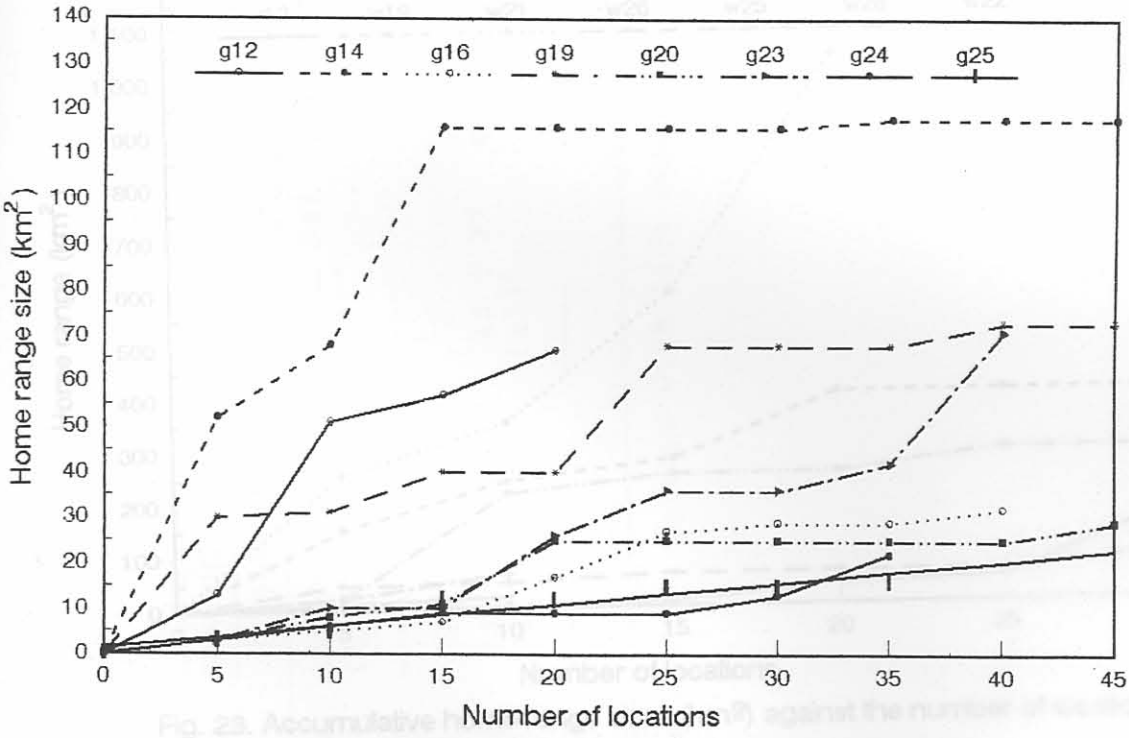

Fig. 21. Accumulative home range sizes (km2) against the number of locations for individual gemsbok males.

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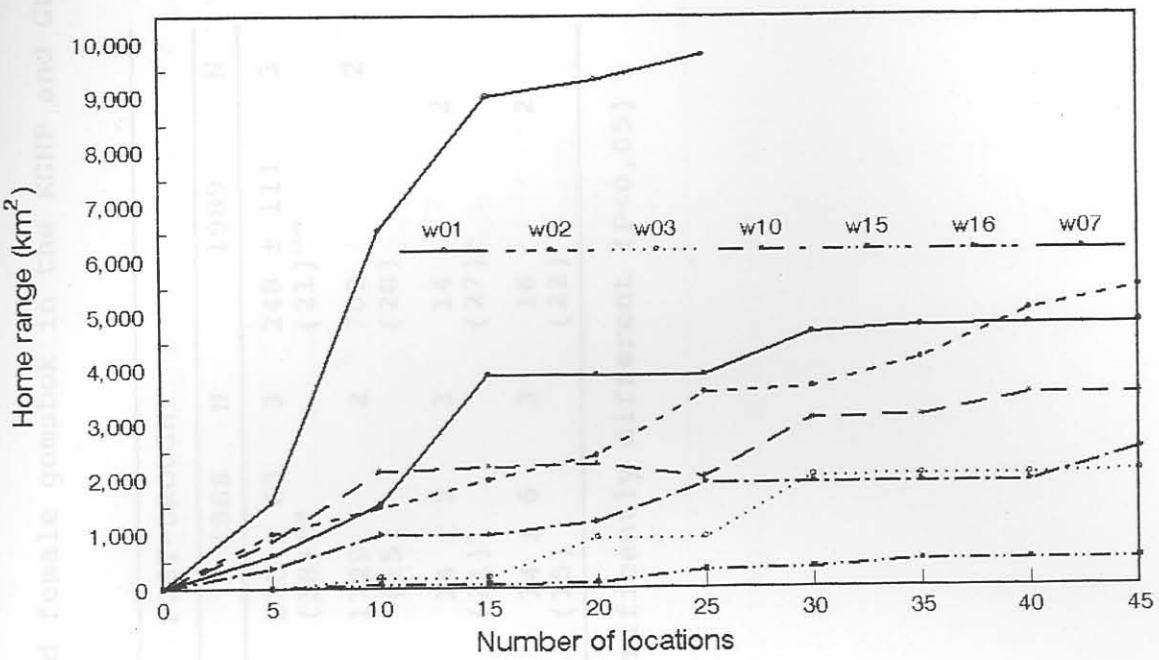

Fig. 22. Accumulative home range sizes (km2) against the number of locations for individual wildebeest females.

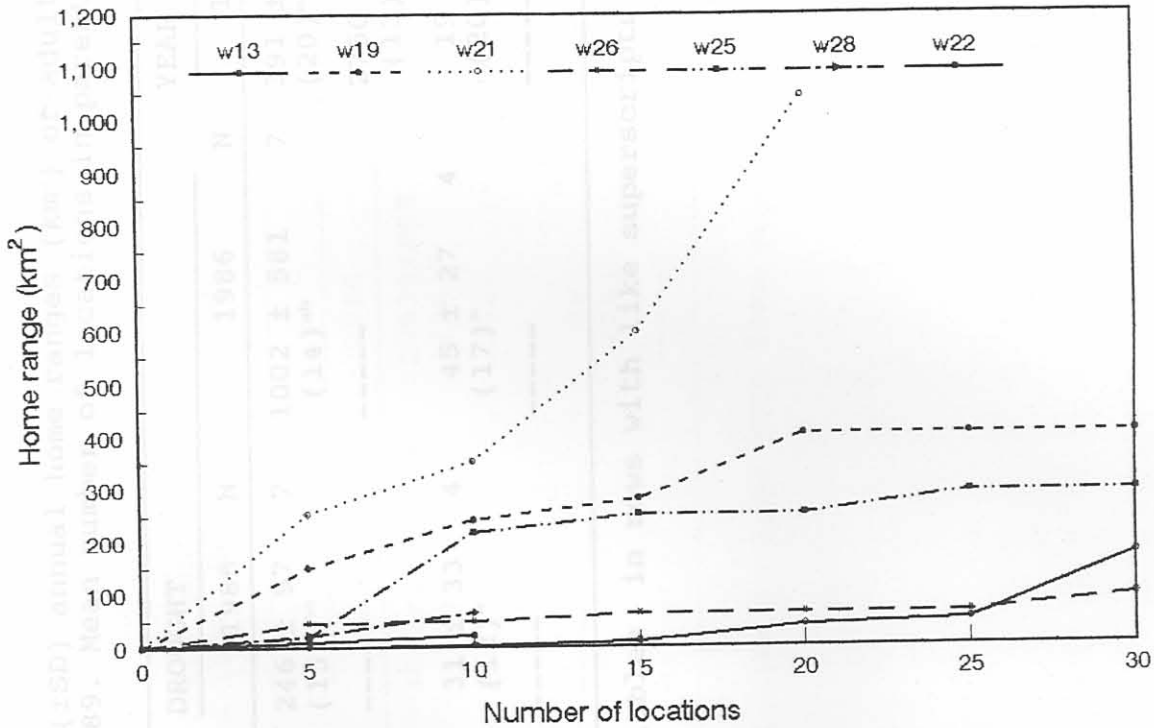

Fig. 23. Accumulative home range sizes (km2) against the number of locations for individual wildebeest males.

Table 21. Mean (±SD) annual home ranges (km^2) of adult male and female gemsbok in the KGNP and GNP from 1985 to 1989. Mean number of locations in parentheses.

SEX	AREA	DROUGHT YEAR 1985	N	1986	N	POST-DROUGHT 1987	N	1988	N	1989	N
♀	KGNP	246 ± 97 (15)[abc]	7	1002 ± 581 (14)[ab]	7	391 ± 54 (20)[ab]	4	278 ± 63 (18)[abd]	3	248 ± 111 (21)[abd]	3
	GNP	-----		-----		2750 (13)	3	1729 (15)	2	702 (20)	2
♂	KGNP	31 ± 33 (12)[a]	4	45 ± 27 (17)[b]	4	19 ± 7 (20)[c]	4	14 ± 3 (21)[d]	3	14 (27)[e]	2
	GNP	-----		-----		-----		14 ± 6 (15)	3	16 (22)	2

Home range variables in rows with like superscripts were significantly different ($P<0,05$)

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Table 22. Mean (±SD) annual home ranges (km^2) of adult male and female wildebeest in the KGNP and GNP from 1985 to 1989. Mean (±SD) number of locations in parentheses.

SEX	AREA	YEAR									
		1985	N	1986	N	1987	N	1988	N	1989	N
♀	KGNP	3643±2186 (18)[a]	5	2063±1065 (24)[b]	4	305 (21)	2	1162±627 (23)[abc]	3	917 (29)	2
	GNP	-----		-----		-----		-----		2649 (15)	1
♂	KGNP	-----		38 (16)	2	427±159 (28)[a]	3	234±163 (24)[a]	3	70±27 (20)[c]	4
	GNP	-----		-----		-----		-----		-----	

Home range variables in rows with like superscripts were significantly different (P<0,05).

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Annual Home Ranges

Average annual home range sizes of adult females of both species were larger than those of the males in all years (F test; $P<0,05$), except for wildebeest in 1986 when an insufficient number of male estimates were obtained (Tables 21 & 22; Figs 24-27). Although the home ranges of both male and female wildebeest were generally larger than those of the same gemsbok sexes, the differences were only significant in 1988 ($F=5,17$; $df=8$; $P=0,05$) and 1985 ($F=24,8$; $df=11$; $P=0,0006$).

The predominant area of residence also appeared to influence mean annual home range sizes. Gemsbok females that remained for the majority of their time in the GNP had average annual ranges of 2067 ± 1241 km^2 ($\pm$SD) ($N=9$), that were significantly ($F=32,5$; $df=29$; $P=0,0001$) larger than the 458 ± 414 km^2 ($\pm$SD) ($N=21$) found for those individuals living predominantly within the KGNP (Table 21; Fig 24b-e). With an increase in rainfall after 1987, a decline in the home ranges of individuals resident in the GNP was evident (refer to female G02 in Figures 24c-e), and furthermore, female G02 also remained permanently in the GNP during 1988 and did not visit the waterholes along the river-bed. In 1989, G02's move nearer to the KGNP waterholes occurred during November 1988, as the rains were unusually delayed until February 1989 (Fig. 24e). Besides yearly variations in home range sizes, individual gemsbok females showed little alteration in core areas used from one year to the next and also demonstrated wide overlap with other individuals (refer to females G08, G13 and G15 (Fig. 24a-e)). While on the contrary, adjacent adult males showed more exclusive use of their ranges (refer to individuals G14, G16 and G20 from 1985-1987 (Fig. 25a)). Figure 25b & c illustrates that male G23 acquired the territory from G16 (which held the territory for a minimum of the previous three years), but during 1988 and 1989 G20 appeared to shift his territory into that of G23 which in turn responded with wider ranging movements in the area.

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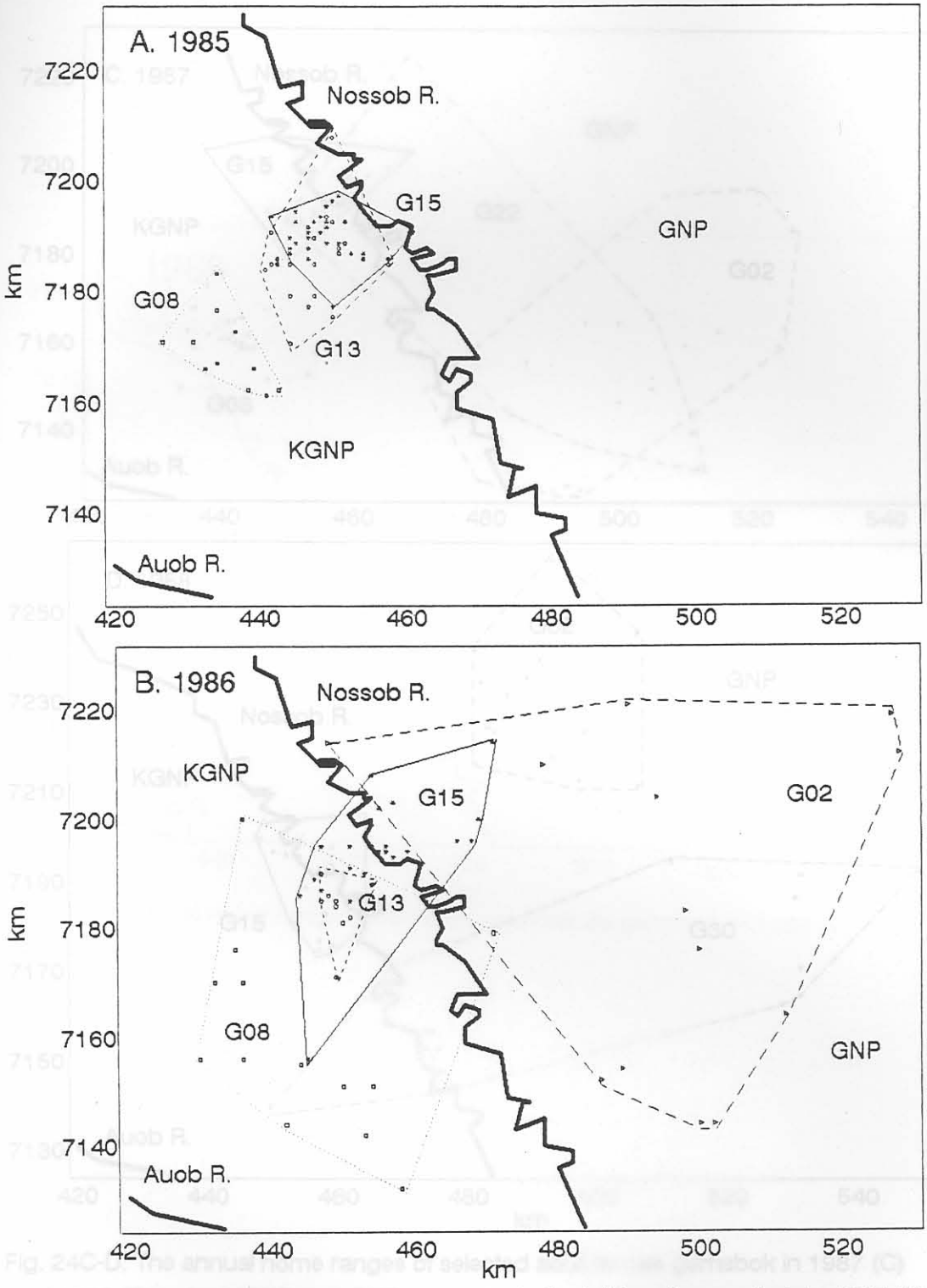

Fig. 24A-B. The annual home ranges of selected adult female gemsbok in 1985 (A) and 1986 (B) in the KGNP and GNP.

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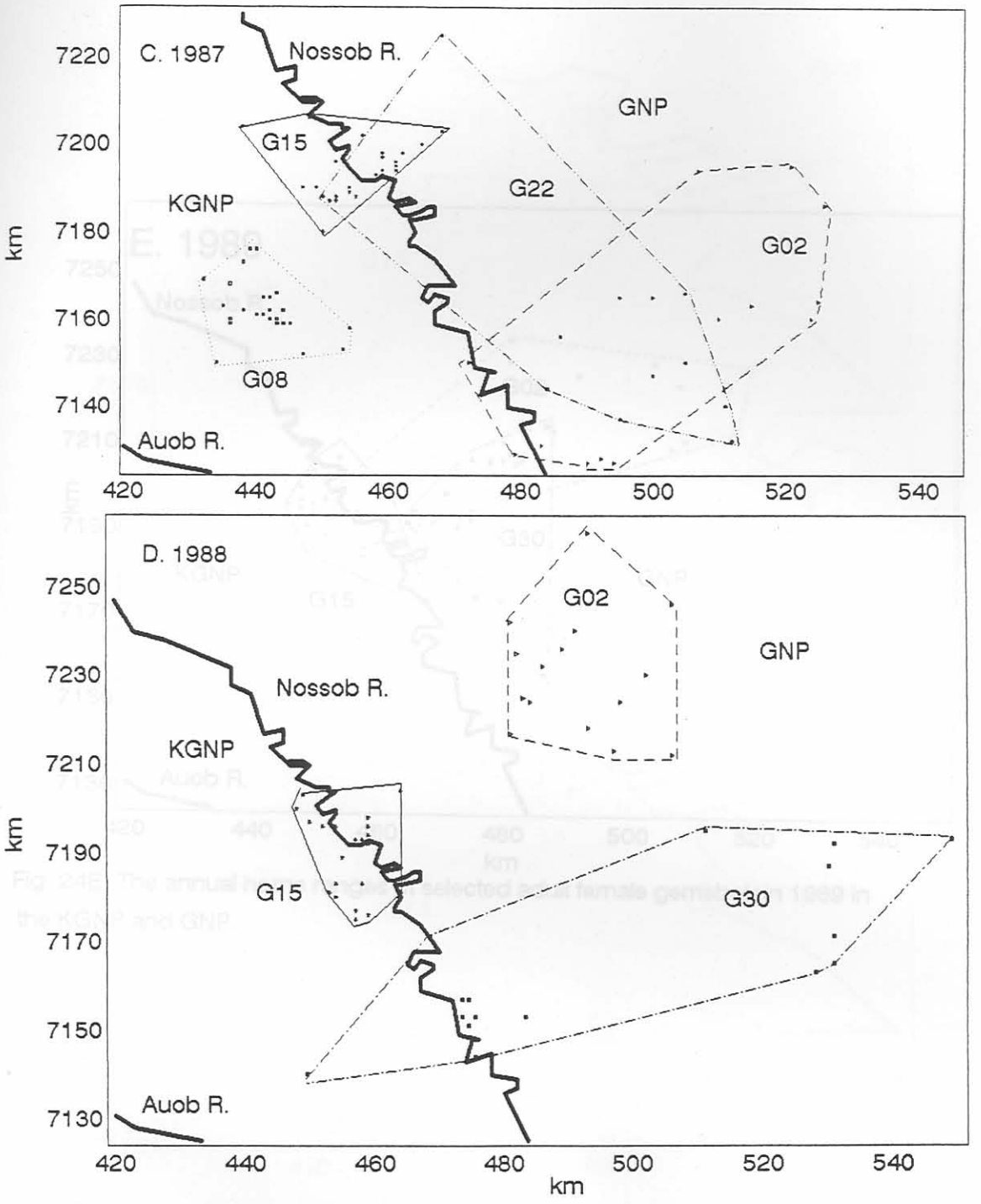

Fig. 24C-D. The annual home ranges of selected adult female gemsbok in 1987 (C) and 1988 (D) in the KGNP and GNP.

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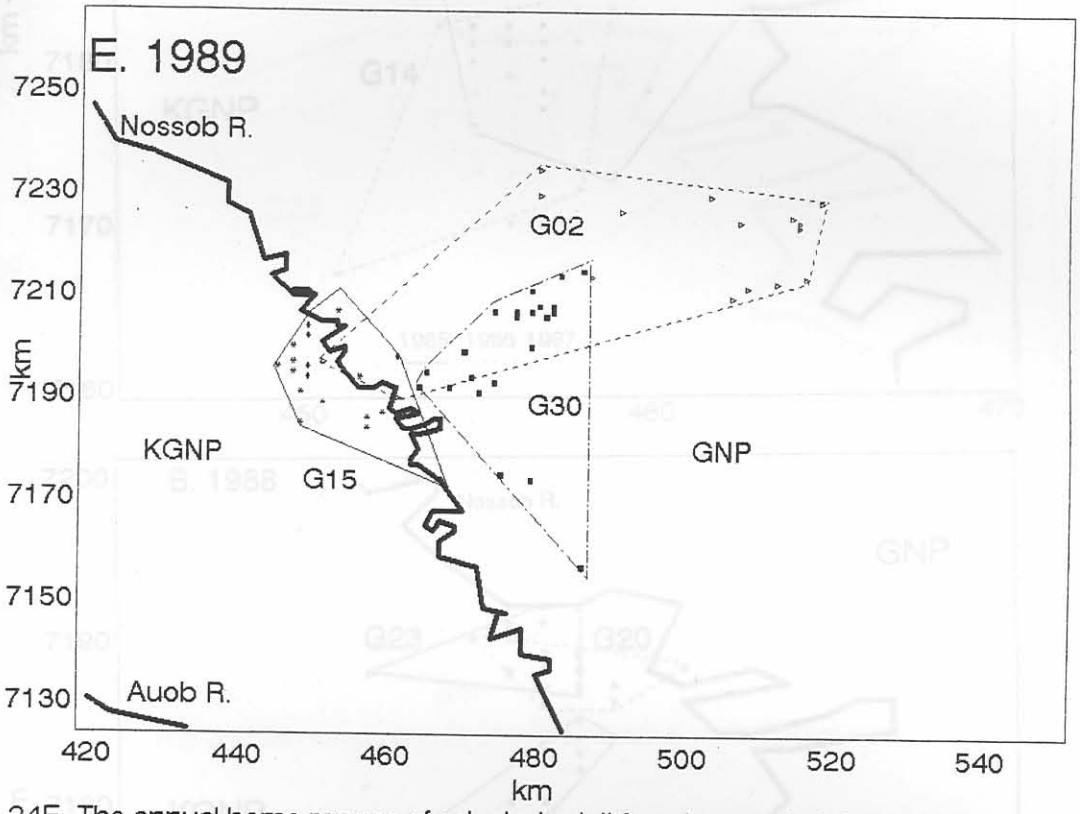

Fig. 24E. The annual home ranges of selected adult female gemsbok in 1989 in the KGNP and GNP.

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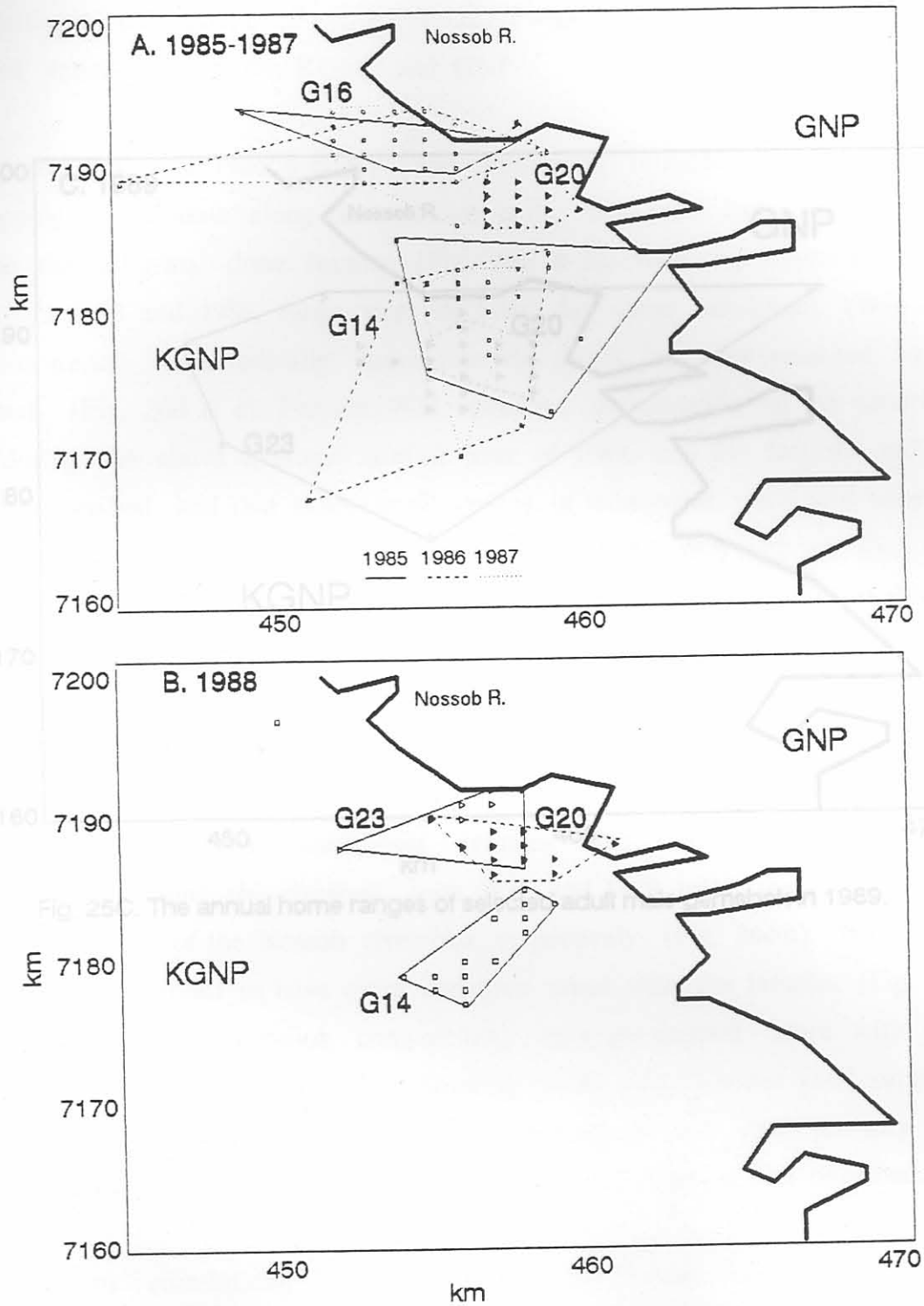

Fig. 25A-B. The annual home ranges of selected adult male gemsbok in A) 1985-1987 and B) in 1988 in the KGNP and GNP. Tracking of G20 began in 1987.

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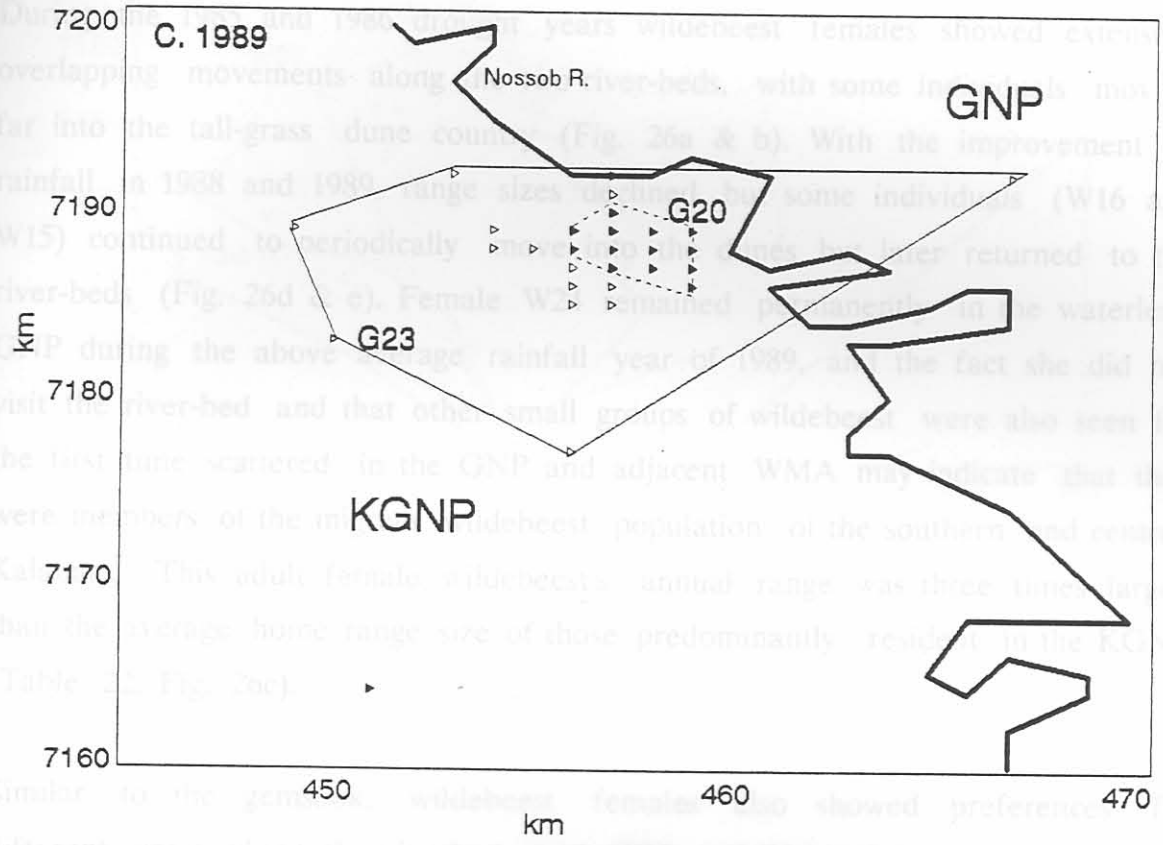

Fig. 25C. The annual home ranges of selected adult male gemsbok in 1989.

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No significant differences ($F=0,54$; $df=22$; $P=0,47$) were found between male gemsbok range sizes in the KGNP and GNP.

During the 1985 and 1986 drought years wildebeest females showed extensive overlapping movements along the two river-beds, with some individuals moving far into the tall-grass dune country (Fig. 26a & b). With the improvement in rainfall in 1988 and 1989, range sizes declined but some individuals (W16 and W15) continued to periodically move into the dunes but later returned to the river-beds (Fig. 26d & e). Female W24 remained permanently in the waterless GNP during the above average rainfall year of 1989, and the fact she did not visit the river-bed and that other small groups of wildebeest were also seen for the first time scattered in the GNP and adjacent WMA may indicate that they were members of the migrant wildebeest population of the southern and central Kalahari. This adult female wildebeest's annual range was three times larger than the average home range size of those predominantly resident in the KGNP (Table 22, Fig. 26c).

Similar to the gemsbok, wildebeest females also showed preferences for different areas along the riverbed, with W15 and W10 using the northern and southern reaches of the Nossob river-bed respectively (Fig. 26c-e). Wildebeest males were also noted to have more exclusive areas than the females (Fig. 27a-d). But unlike their gemsbok compatriots, they overlapped more with their neighbours as a result of moving to drinking water and to better food supplies, such as males W25 and W13 in 1987, which both abandoned their territory core areas (indicated with arrows in Figure 27b & c) to move up the river-bed.

No significant correlations were found between rainfall variables (ie. mean summer rainfall, mean number of storms greater than 10 mm, mean number of days between 10 mm rain storms, and mean number of occurrences of 10 mm storms separated by less than 15 days (see Chapter 2)) and annual home ranges sizes for either of the sexes of the two species.

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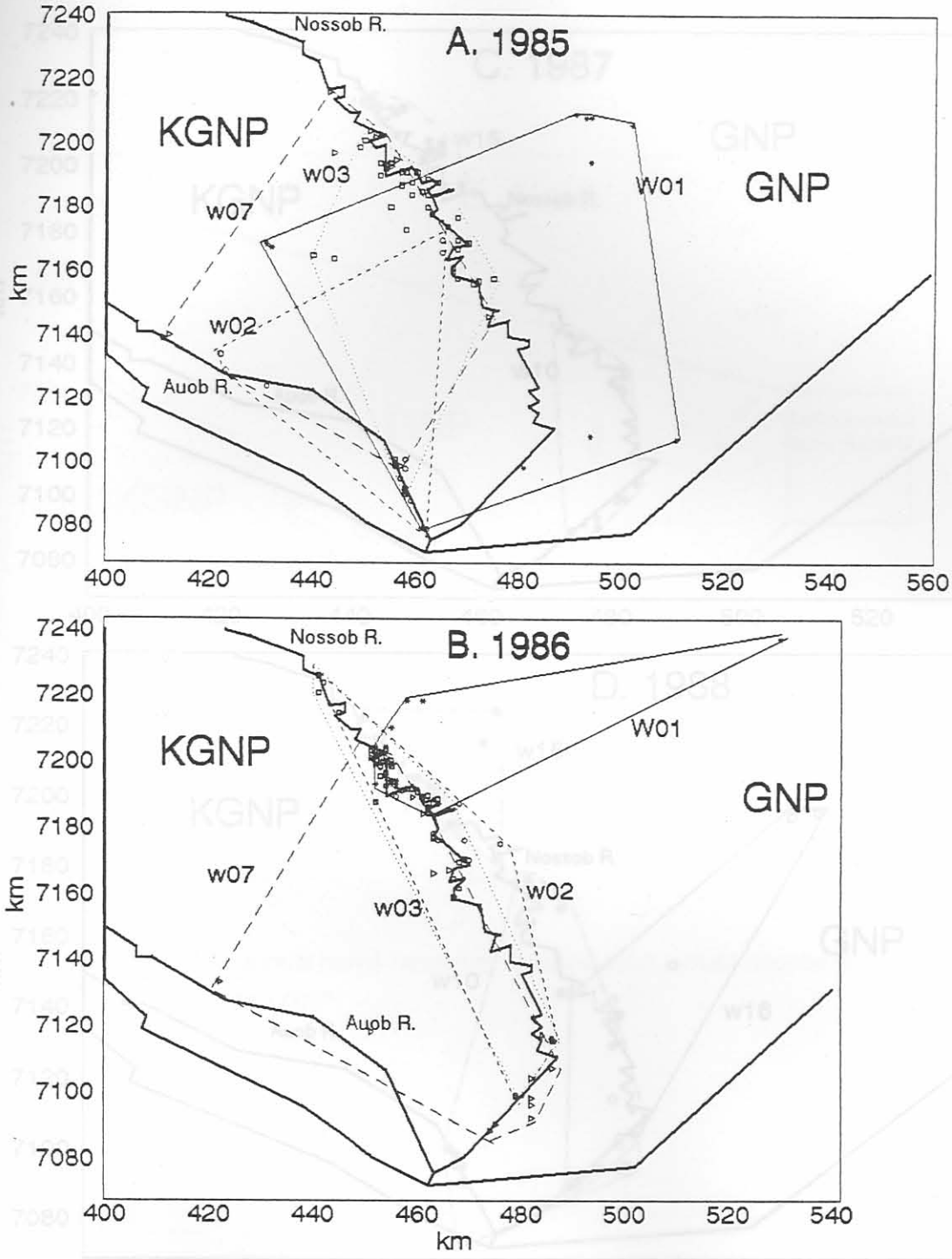

Fig. 26A-B. The annual home ranges of selected adult female wildebeest in 1985 (A) and 1986 (B) in the KGNP and GNP.

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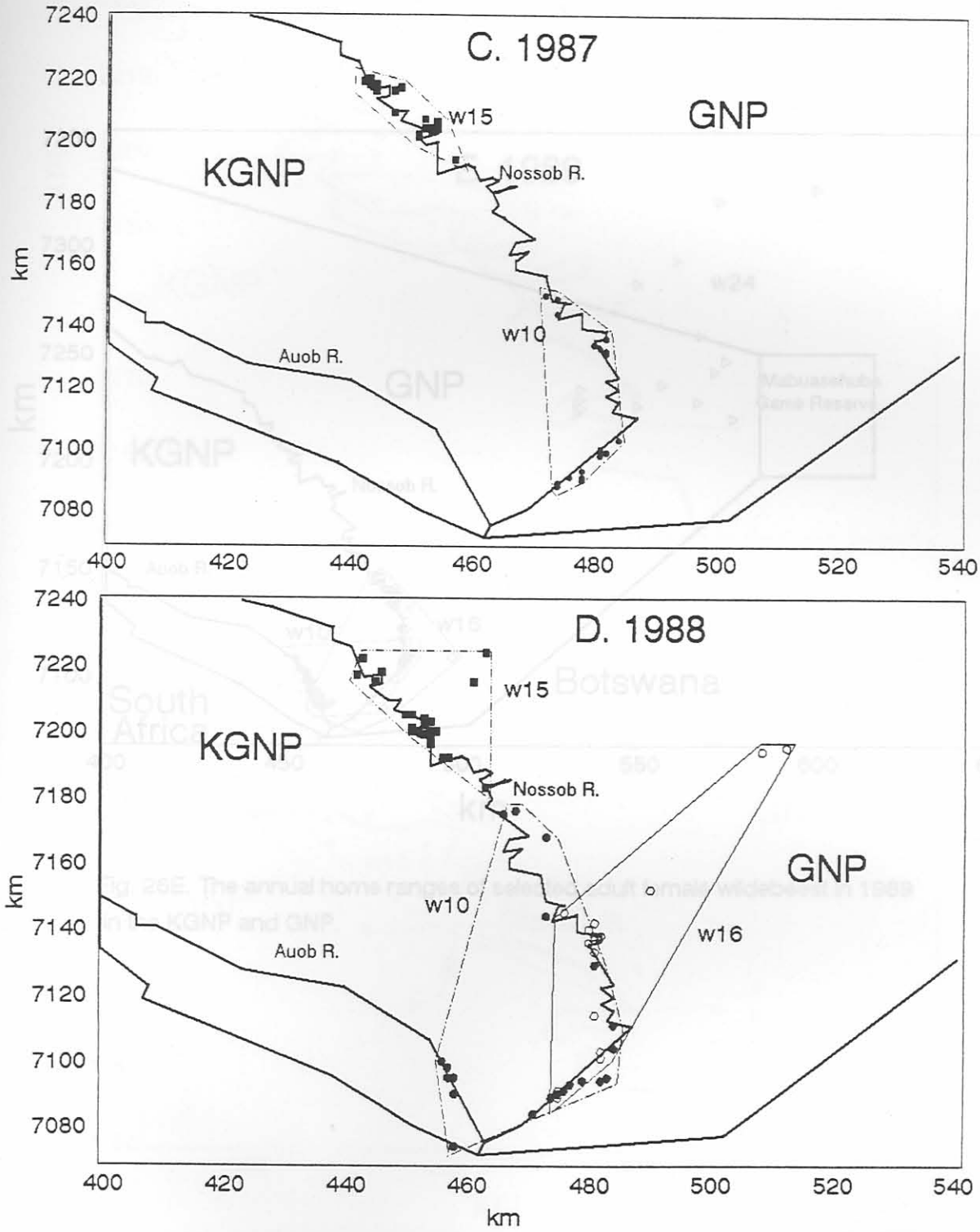

Fig. 26C-D. The annual home ranges of selected adult female wildebeest in 1987 (C) and 1988 (D) in the KGNP and GNP.

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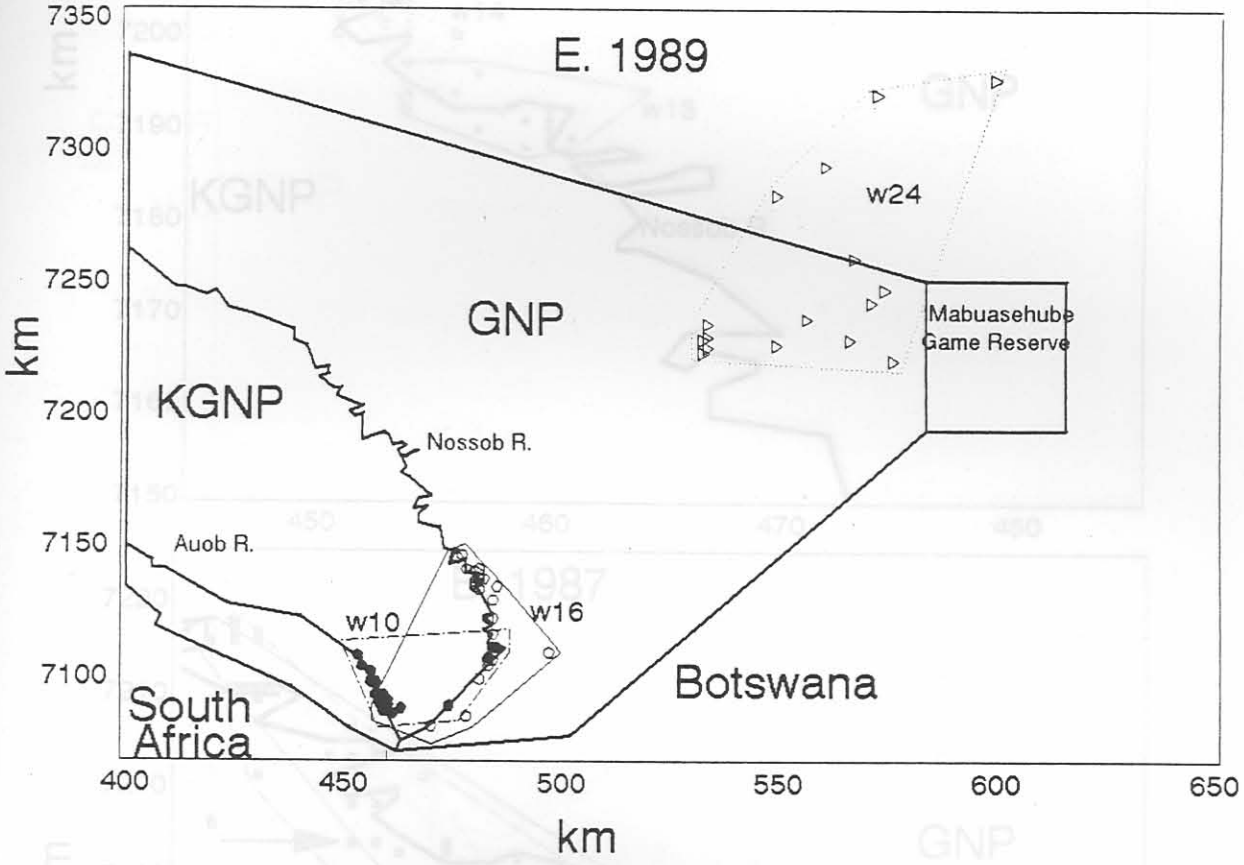

Fig. 26E. The annual home ranges of selected adult female wildebeest in 1989 in the KGNP and GNP.

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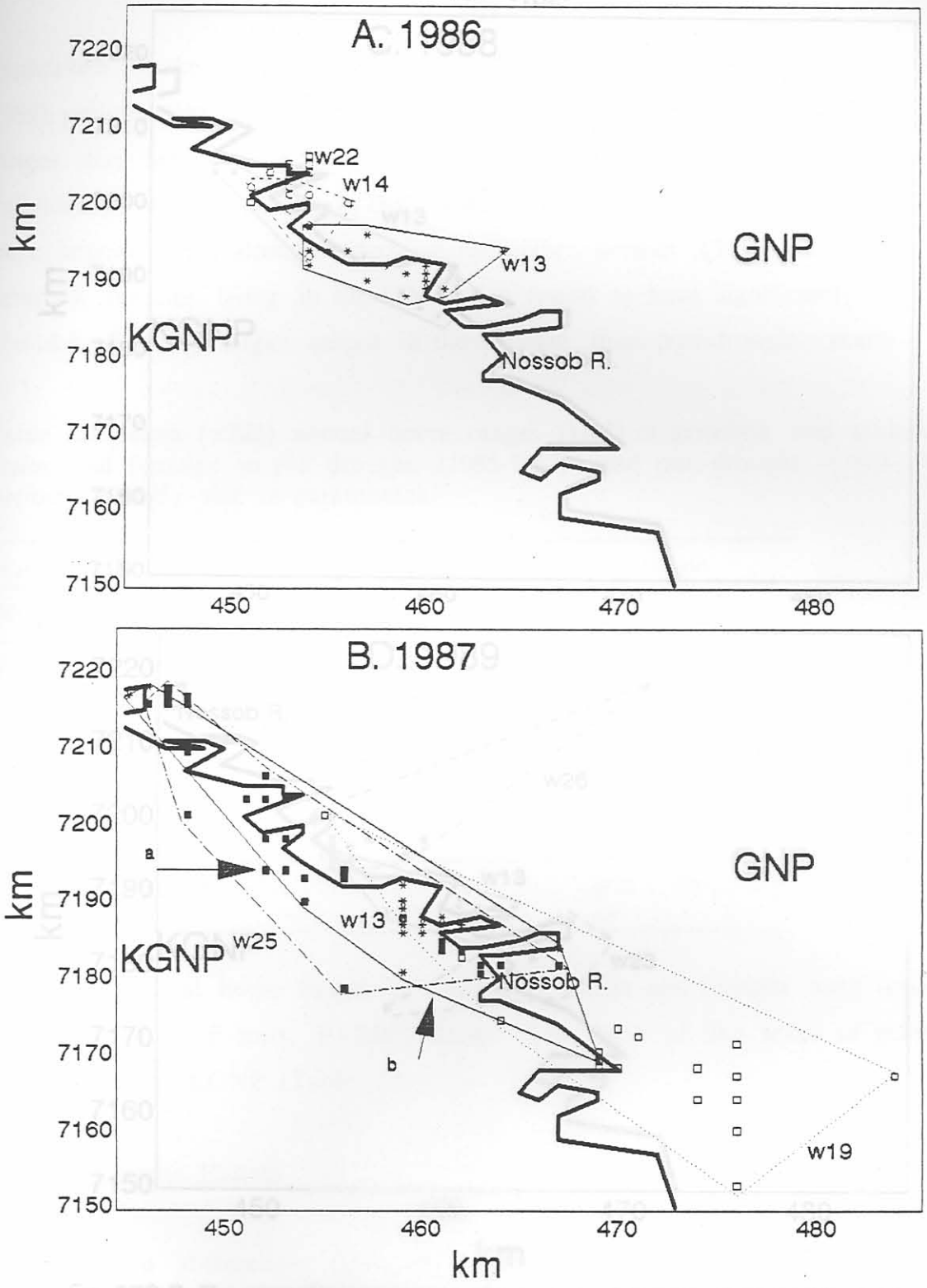

Fig. 27A-B. The annual home ranges of selected adult male wildebeest in 1986 (A) and 1987 (B) in the KGNP and GNP. Arrows a and b indicate core areas for males w25 and w13 respectively.

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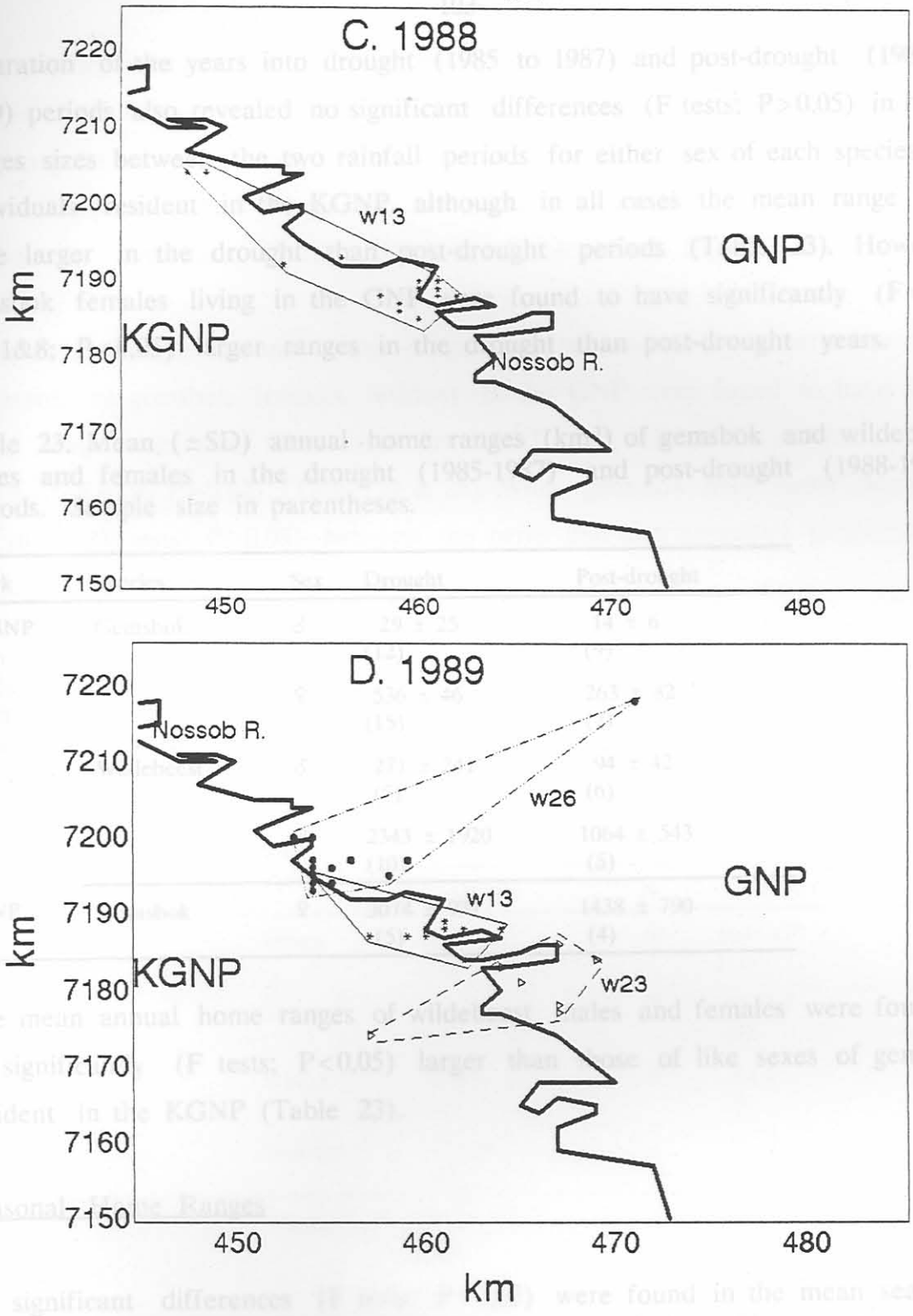

Fig. 27C-D. The annual home ranges of selected adult male wildebeest in 1988 (C) and 1989 (D) in the KGNP and GNP.

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Separation of the years into drought (1985 to 1987) and post-drought (1988 to 1989) periods also revealed no significant differences (F tests; $P>0,05$) in home ranges sizes between the two rainfall periods for either sex of each species for individuals resident in the KGNP, although in all cases the mean range sizes were larger in the drought than post-drought periods (Table 23). However, gemsbok females living in the GNP were found to have significantly ($F=5,5$; $df=1\&8$; $P<0,05$) larger ranges in the drought than post-drought years.

Table 23. Mean (±SD) annual home ranges (km^2) of gemsbok and wildebeest males and females in the drought (1985-1987) and post-drought (1988-1989) periods. Sample size in parentheses.

Park	Species	Sex	Drought	Post-drought
KGNP	Gemsbok	♂	29 ± 25 (12)	14 ± 6 (9)
		♀	536 ± 46 (15)	263 ± 82 (7)
	Wildebeest	♂	271 ± 241 (5)	94 ± 42 (6)
		♀	2343 ± 1920 (10)	1064 ± 543 (5)
GNP	Gemsbok	♀	3074 ± 931 (5)	1438 ± 790 (4)

The mean annual home ranges of wildebeest males and females were found to be significantly (F tests; $P<0,05$) larger than those of like sexes of gemsbok resident in the KGNP (Table 23).

Seasonal Home Ranges

No significant differences (F tests; $P>0,05$) were found in the mean seasonal home range sizes for each sex and species using all five years data. Although the seasonal ranges tended to be larger in the drought than post-drought periods for both species and sexes, only a few of the comparisons were found to be statistically significant (Tables 24 & 25).

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Interspecific comparisons of the seasonal ranges revealed in all cases that the ranges of adult male and female wildebeest exceeded those found for male and female gemsbok, respectively. But owing to the large variations in the data, only the wildebeest male ranges in both rainfall periods were found to be statistically significant (F tests; $P<0.05$) (Tables 24 & 25)

Differences in the seasonal home range sizes between the two parks were also different, as gemsbok females resident in the GNP were found to have larger home range sizes than those from the KGNP, but only in the summer months ($F=6,1$; $df=19$; $P=0,02$) (Table 24 & 25). While gemsbok male home ranges did not differ (F tests; $P>0,05$) between the parks and also appeared unaffected by season.

Table 24. Mean (±SD) seasonal ranges (km^2) of adult male and female gemsbok in the KGNP and GNP during the drought (1985 to 1986) and post-drought (1987 to 1989) periods. Mean number of locations per individual in parentheses.

Area	Sex	Season	Drought		Post-Drought	
			MEAN	N	MEAN	N
KGNP	♀	Winter	287±344 (13)	10	169±47[a] (11)	6
		Summer	218±148 (10)	5	90±46[a] (8)	5
	♂	Winter	13±5 (12)	5	6±3 (9)	4
		Summer	14±18 (9)	4	12±6 (13)	5
GNP	♀	Winter	3389 (10)	1	548±598 (9)	4
		Summer	---	--	1116±942 (9)	4
	♂	Winter	------	--	9±6 (10)	5
		Summer	------	--	3 (10)	2

Between season comparisons for each sex with like superscripts in columns were significantly different (F test; $P<0,05$).

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Table 25. Mean (±SD) seasonal ranges (km^2) of adult male and female wildebeest in the KGNP and GNP during the drought (1985 to 1986) and post-drought (1987 to 1989) periods. Mean number of locations per individual in parentheses.

Area	Sex	Season	Drought		Post-Drought	
			Mean	N	Mean	N
KGNP	♀	Winter	634±603 (14)	8	342±282 (11)	5
		Summer	734±732 (11)	8	585±165 (13)	5
	♂	Winter	95±66 (15)	4	27±32 (14)	4
		Summer	91±115 (10)	4	75±35 (17)	3
GNP	♀	Winter	------	--	1689 (11)	1
		Summer	------	--	------	--
	♂	Winter	------	--	------	--
		Summer	------	--	------	--

Male Territoriality

Territorial wildebeest and gemsbok males, as defined by Estes (1969) and Wacher (1986) and accepted in this study, are those individuals which generally defend their own small home ranges (in comparison to non-territorial males and adult females) through threat demonstration, fighting and marking.

The mean group size of radio-collared territorial gemsbok and wildebeest bulls were 3,9±6,8 (±SD) (n=322) and 11,0±20,0 (±SD) (n=178) respectively, and significantly smaller than the 11,9±13,8 (±SD) (n=401) ($F=328,2$; $df=1\&722$; $P<0,001$) and 37,8±6,8 (±SD) (n=178) ($F=284,1$; $df=1\&541$; $P<0,001$) found for gemsbok and wildebeest females, respectively. Only one radio-collared gemsbok male (no. 31) was considered non-territorial, as he ranged over a larger area (Table 20) and associated with larger groups of 17,4±13,8 (±SD)

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(n=16) individuals than the territorial males. Territorial males of gemsbok and wildebeest were noted to be solitary on 57,1% (n=322) and 49,4% (n=178) of observations respectively, while only in 6,2% (n=16) of observations was the non-territorial gemsbok male noted to be alone. No non-territorial wildebeest males were radio-collared, although periodically territorial males consorted with bachelor groups for short periods and later returned to their territories.

Territorial disputes between neighbouring gemsbok males were witnessed on two occasions. In the one instance the study animal (no. G16) tried to block a small herd of females from moving into the next territory while on the territory boundary. The neighbouring bull witnessed the blocking action and once the blocking male actually breached the boundary, the defender instigated an aggressive encounter which he won and drove the infiltrator (no. G16) 300 m back into his territory.

As the vast majority of the radio locations were made from the air, the consistent use of a small area and a tendency to remain solitary were taken as indicative of territorial status in males of both species.

Between Location Distances

Distances between consecutive sightings were also used as an index for animal movement (Table 26). Gemsbok and wildebeest sightings averaged 10,3±6,7 (±SD) (n=926) and 8,6±6,2 (±SD) (n=688) days apart, respectively. Intraspecific comparisons revealed significantly greater distances for gemsbok females (Wilcoxon matched pairs; T=1,99; P=0,05) in the post-drought period than during the drought, while no interspecific differences were detected between like sexes in either of the two rainfall periods (Wilcoxon matched pairs; T test; P>0,05).

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Table 26. Distance (km±SD) between locations, corrected for by day, for both gemsbok and wildebeest sexes in the summer and winter of the drought (1985-1987) and post-drought periods (1988-1989).

Species	Sex	Season	Distance moved (km/day)			
			Drought	N	Post-drought	N
Gemsbok	♂	Summer	1,8 ± 2,9	41	0,9 ± 1,8	98
		Winter	2,4 ± 12,2	54	3,4 ± 9,9	111
	♀	Summer	2,8 ± 3,5	66	4,6 ± 7,4	69
		Winter	3,6 ± 4,9	85	7,6 ± 20,3	112
Wildebeest	♂	Summer	1,3 ± 1,5	20	2,3 ± 5,0	60
		Winter	1,3 ± 1,7	31	1,4 ± 2,3	60
	♀	Summer	5,2 ± 6,0	69	6,7 ± 14,1	68
		Winter	6,8 ±14,6	88	4,2 ± 4,9	112

Seasonal differences were only found for gemsbok, with both the males (Wilcoxon matched pairs; T=-2,06; P=0,04) and females (Wilcoxon matched pairs; T=-2,03; P=0,04) having larger inter-location distances in the winter than summer months.

Similar to the differences found in home range sizes for gemsbok between the two adjoining parks, female gemsbok within the GNP were also noted to have significantly (Wilcoxon matched pairs; T=2,33; P=0,019) larger inter-location distances of 5,6±14,8 (±SD) km in the waterless GNP in comparison to 4,8±12,0 (±SD) km in the KGNP. No significant (Wilcoxon matched pairs; T=-1,6; P=0,113) differences were found in the inter-location distances for gemsbok males in either parks.

Association with Waterholes

Male and female gemsbok were found to range at greater distances from waterholes than wildebeest during and after the drought (Table 27). Females of both species were always found further afield from water than the males. Improvement of rainfall in the post-drought period resulted in both species and

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sexes, except wildebeest territorial males, moving further from available drinking water. While no seasonal differences in the distances were found for either species or sex (F tests; $P<0,05$).

Table 27. Mean distances (km±SD) to the nearest waterhole for male and female gemsbok and wildebeest in the drought (1985-1986) and post drought period. (1987-1989).

Species	Sex	Distance To Water (km)			
		Drought	N	Post-Drought	N
Gemsbok	♂	3,9± 2,7a*	158	9,3±13,8a*	242
	♀	9,1±13,0a*	239	13,9±17,5a*	287
Wildebeest	♂	3,0± 2,8a*	70	2,4± 2,6a*	156
	♀	6,3±12,2*	224	9,3±24,3*	238

*Values in rows with like superfixes were significantly different ($P<0,05$).

The quality of the water available in the drinking troughs also appeared to influence the two species association with the waterholes. Wildebeest were found significantly ($\chi^2=5,04$; $df=1$; $P=0.025$) more often drinking at the fresh than at saline and hypersaline waterholes, while the gemsbok showed no differences ($\chi^2=0,30$; $df=1$; $P=0,587$). Analysis of the distance data in relation to waterhole water quality, revealed that both species were significantly further from the hypersaline than the fresh and saline waterholes (Table 28).

Table 28. Mean distances (km±SD) to the closest waterholes of different quality (f=fresh; s=saline; h=hypersaline) by gemsbok and wildebeest males and females.

Species	Sex	Distances to water (km)					
		Fresh	N	Saline	N	Hyper-saline	N
Gemsbok	♂	$4,2\pm 7,8^b$	225	$4,0\pm 3,1^b$	26	$23,1\pm 19,6^a$	222
	♀	$10,6\pm 13,8^b$	259	$4,9\pm 10,6^a$	58	$15,0\pm 19,1^b$	209
Wildebeest	♂	$2,4\pm 2,3^a$	188	$3,3\pm 2,8^a$	37	9,4	1
	♀	$4,0\pm 2,8^b$	215	$2,8\pm 2,0^b$	58	$13,7\pm 29,2^a$	189

Value in rows with differing superfixes were significantly different ($P<0,05$).

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Habitat Selection

Gemsbok showed variations in their seasonal habitat preferences, with habitat '4' (Acacia haematoxylon on dunes) being selected for in the cold-dry and hot-dry seasons, while habitat '1' (tree savanna) was avoided in the hot-dry and hot-wet summer seasons (Table 29). On the other hand, wildebeest showed a preference and avoidance for habitats '2' (riverine) and '1' respectively, in all seasons (Table 30).

Comparisons between the drought and post-drought periods revealed a lack of selection by gemsbok in the latter period, while in the drought they showed more avoidance and selection for habitats '1' and '4' respectively, similar to that found above (Table 31). Wildebeest showed similar responses in the two periods with respect to avoiding and preferring habitats '1' and '2' respectively (Table 31).

No seasonal differences in the frequency of community use by gemsbok were found ($X^2 = 12,8$; $df = 10$; $P = 0,236$) (Table 32). They did however consistently use communities '3' and '4' more than their proportional availability. The wildebeest's community use did differ significantly ($X^2 = 22,91$; $df = 10$; $P = 0,011$) and probably arises from their greater use of communities '4' and '13' in the cold-dry season (Table 32). Throughout the three seasons wildebeest used the short grass riverine communities '6' and '7' in greater proportions than availability, similar to that found in the habitat analysis above (Table 30).

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Table 29. Seasonal habitat selection by gemsbok. A or P = significantly (P<0,05) avoiding or preferring habitat respectively and -=no selection. Habitats: 1=tree savanna; 2=river; 3=B. albitrunca on dunes; 4=A. haematoxylon on dunes; 5=A. haematoxylon on plains; 6=braks and pans.

Season	Habitat	% Available Habitat (P)	No. Locations	% Locations	95 % Confidence	A or P
	1	60,07	169	50,8	0,609≥ P ≥ 0,406	-
	2	5,07	12	3,6	0,177≥ P ≥-0,105	-
COLD-	3	10,01	41	12,3	0,258≥ P ≥-0,012	-
DRY	4	11,73	82	24,6	0,371≥ P ≥ 0,120	P
	5	12,92	19	5,7	0,198≥ P ≥-0,083	-
	6	0,21	10	3,0	0,172≥ P ≥-0,112	-
	1	60,07	139	40,1	0,510≥ P ≥ 0,290	A
	2	5,07	16	4,6	0,184≥ P ≥-0,092	-
HOT-	3	10,01	64	18,4	0,312≥ P ≥ 0,057	-
DRY	4	11,73	90	25,9	0,381≥ P ≥ 0,138	P
	5	12,92	23	6,6	0,203≥ P ≥-0,071	-
	6	0,21	15	4,3	0,182≥ P ≥-0,095	-
	1	60,07	148	49,0	0,598≥ P ≥ 0,382	A
	2	5,07	17	5,6	0,204≥ P ≥-0,091	-
HOT-	3	10,01	39	12,9	0,271≥ P ≥-0,013	-
WET	4	11,73	67	22,2	0,355≥ P ≥0,088	-
	5	14,92	16	5,3	0,142≥ P ≥-0,083	-
	6	0,21	15	5,0	0,198≥ P ≥-0,098	-

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Table 30. Seasonal habitat selection by wildebeest. A and P=significantly (P<0,05) avoiding or preferring habitat respectively and -= no selection; *=sample too small to calculate intervals. Habitats: 1=tree savanna; 2=river; 3=B. albitrunca on dunes; 4=A. haematoxylon on dunes; 5=A. haematoxylon on plains; 6=braks and pans.

Season	Habitat	% Available Habitat (P)	No. Locations	% Locations	95 % Confidence	A or P
	1	60,07	74	34,43	0,488≥ P ≥ 0,197	A
	2	5,07	126	58,3	0,699≥ P ≥ 0,467	P
COLD-	3	10,01	5	2,3	0,200≥ P ≥-0,154	-
DRY	4	11,73	1	0,5	*	*
	5	12,92	3	1,4	*	*
	6	0,21	7	3,2	0,209≥ P ≥-0,144	-
	1	60,07	71	32,3	0,469≥ P ≥0,176	A
	2	5,07	126	57,3	0,689≥ P ≥0,456	P
HOT-	3	10,01	3	1,4	*	*
DRY	4	11,73	8	3,6	0,211≥ P ≥-0,138	-
	5	12,92	2	0,9	*	*
	6	0,21	10	4,6	0,219≥ P ≥-0,128	-
	1	60,07	51	23,7	0,394≥ P ≥0,080	A
	2	5,07	153	71,2	0,808≥ P ≥0,615	P
HOT-	3	10,01	1	0,5	*	*
WET	4	11,73	5	1,9	0,197≥ P ≥-0,180	-
	5	12,52	5	1,9	0,197≥ P ≥-0,160	-
	6	0,21	2	0,9	*	*

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Table 31. Seasonally avoided and preferred habitats of gemsbok and wildebeest in the drought (1985 to 1986) and post-drought (1987 to 1989) periods. Numbers (see Table 29) refer to habitat type significantly ($P<0,05$) avoided or preferred. CD = cold-dry season; HD = hot-dry season and HW = hot-wet season.

Species	Season	Drought		Post-drought	
		Prefer	Avoid	Prefer	Avoid
Gemsbok	CD	---	---	---	---
	HD	4	1	---	---
	HW	---	1	---	---
Wildebeest	CD	2	---	2	1
	HD	2	1	2	1
	HW	2	1	2	1

Table 32. Use of communities* (%) in the three seasons by gemsbok and wildebeest. Available refers to proportion of communities available. CD = cold-dry, HD = hot-dry, HW = hot-wet.

Species	Season	Community						N	Test
		1	3	4	6	7	13		
AVAILABLE		**11,0**	**36,3**	**4,7**	**0,3**	**0,7**	**44,8**		
Gemsbok	CD	14,7	47,1	20,9	2,2	0,9	14,2	225	$\chi^2 = 12,8$
	HD	14,6	47,9	26,0	2,1	1,6	7,8	192	df = 10
	HW	15,8	42,1	23,4	6,4	1,2	11,1	171	P = 0,236
Wildebeest	CD	0,7	7,0	24,5	40,6	16,8	10,5	143	$\chi^2 = 22,91$
	HD	3,2	10,6	19,4	46,9	15,0	5,0	160	df = 10
	HW	1,6	2,5	15,6	54,1	23,0	3,3	122	P = 0,011

* Communities: 1 = Stipagrostis amabilis, and Stipagrostis amabilis - Terminalia sericea type; 3 = Hirpicio echini - Centropodium glauca type; 4 = Monechma incanum - Stipagrostis ciliata (braks and and river dunes); 6 = Peliostomium leucorrhizum - Stipagrostis obtusa; 7 = Panicum coloratum, Aizoon shellenbergii - Indigofera auricoma, and all pan community types; 13 = Schmidtia kalahariensis, and Schmidtia pappophoroides - Stipagrostis uniplumis.

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Habitat quality variables such as the grass condition, grass density and grass height (Figs 28 & 29), and annual condition differed between seasons and species. Gemsbok appeared to select for generally greener grass conditions (particularly in the hot-dry and hot-wet seasons) than available (Fig. 28a), while the wildebeest associated more with browner grasses than available (Fig. 29a). Gemsbok differed in their selection of grass density and height from wildebeest in more frequently associating with generally denser and taller grass conditions than wildebeest (Figs 28 & 29). Wildebeest showed a notable shift to the taller grasses during the cold-dry and hot-dry seasons. Gemsbok appeared unaffected by ephemeral dicot conditions, except in the hot-wet season when they associated more with ephemerals of middling to good condition than available ($\chi^2 = 14{,}8$; df = 5; $P < 0{,}05$), while the wildebeest appeared to prefer either no

Table 33. Frequency of occurrence (%) of male and female wildebeest (Wild) and gemsbok (Gem) in different greenness classes in the general veld (COND), grass (GCON) and ephemeral dicot (ACON) condition categories. Greenness classes for COND : 1= brown; 2=green tint; 3=fully green. Greenness classes for GCON and ACON: 1=brown; 2=¼ green; 3=½ green; 4=¾ green; 5=fully green.

Veld Variable	Species	Sex	Greenness 1	2	3	4	5	N	Test
COND	Gem	♂	66,6	16,3	17,2	--	--	449	$\chi^2 = 11{,}0$; P = 0,004
		♀	64,2	23,7	12,1	--	--	506	
	Wild	♂	70,7	15,9	13,4	--	--	201	$\chi^2 = 1{,}9$; P = 0,370
		♀	66,1	20,6	13,3	--	--	437	
GCON	Gem	♂	12,9	33,7	23,3	10,4	19,7	249	$\chi^2 = 13{,}2$; P0,010
		♀	11,2	34,5	34,8	8,1	11,5	286	
	Wild	♂	20,5	19,3	25,3	10,8	24,7	83	$\chi^2 = 3{,}4$; P = 0,490
		♀	30,0	17,6	23,8	10,9	17,6	210	
ACON	Gem	♂	27,6	16,8	14,2	7,3	34,1	232	$\chi^2 = 9{,}3$; P = 0,050
		♀	27,1	18,6	20,3	8,5	23,8	247	
	Wild	♂	26,9	19,2	12,8	7,7	33,3	78	$\chi^2 = 3{,}7$; P = 0,454
		♀	36,2	14,1	14,1	4,3	31,3	185	

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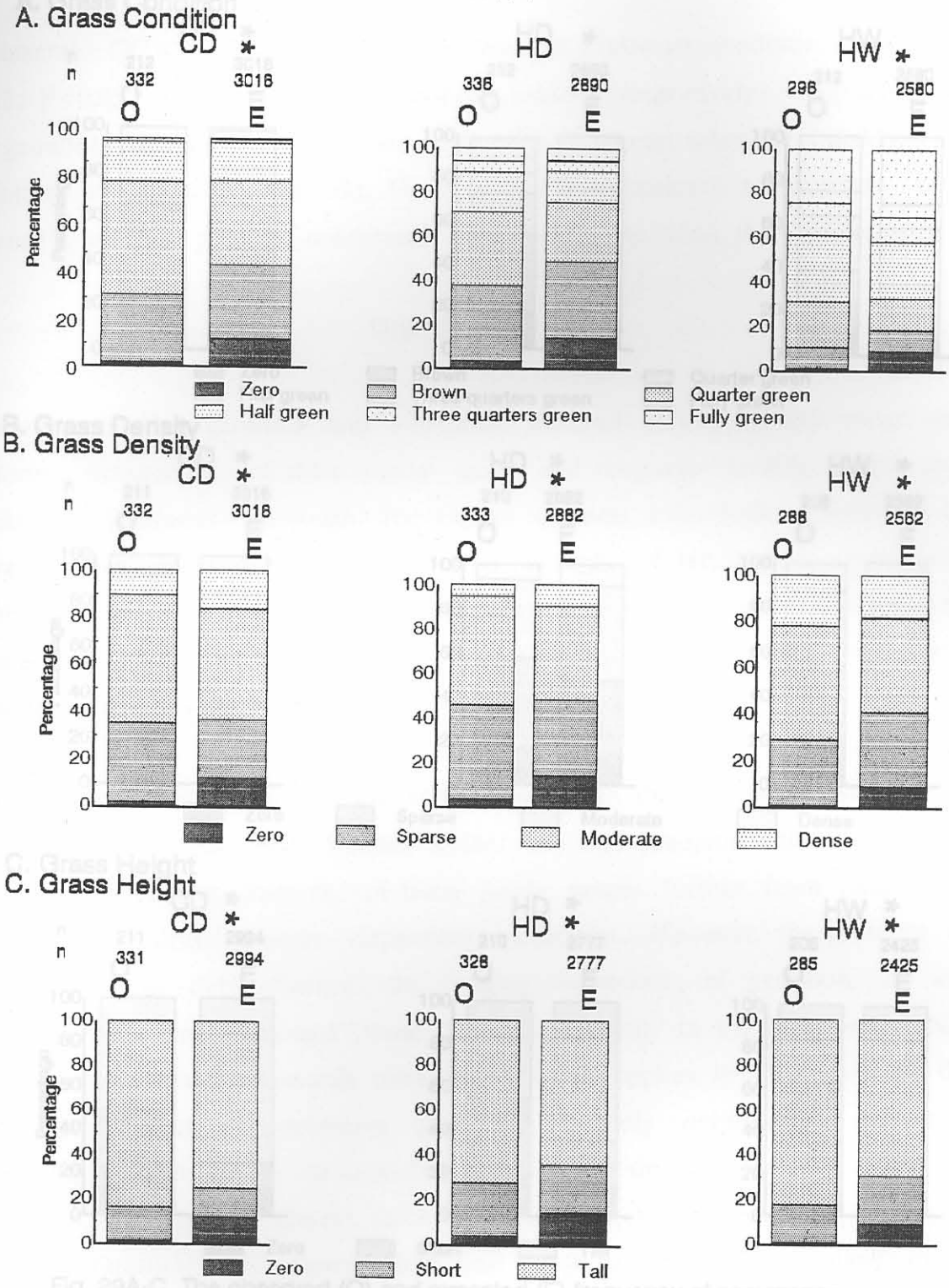

Fig. 28A-C. The observed (O) and expected (E) frequency of occurrence of gemsbok with grasses of different (A) condition, (B) density and (C) height in the three seasons in the KGNP and GNP. CD=cold-dry; HD=hot-dry; HW=hot-wet. * significantly different using Chi-square test, $P<0,05$.

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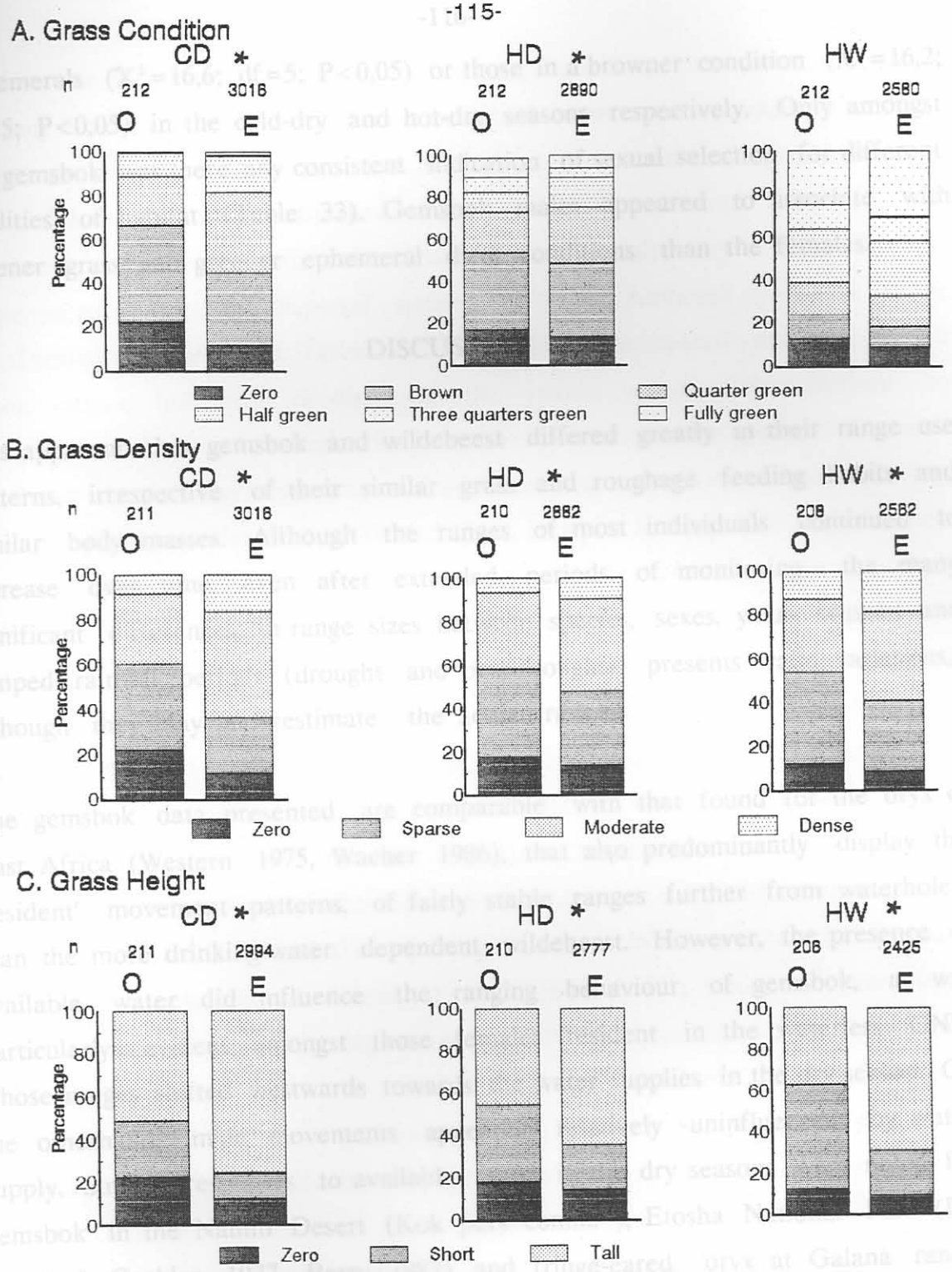

Fig. 29A-C. The observed (O) and expected (E) frequency of occurrence of wildebeest with grasses of different (A) condition, (B) density and (C) height in the three seasons in the KGNP and GNP. CD=cold-dry; HD=hot-dry; HW=hot-wet. * significantly different using Chi-square test, $P<0,05$.

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ephemerals ($X^2 = 16,6$; $df = 5$; $P < 0,05$) or those in a browner condition ($X^2 = 16,2$; $df = 5$; $P < 0,05$) in the cold-dry and hot-dry seasons respectively. Only amongst the gemsbok was there any consistent indication of sexual selection for different qualities of habitat (Table 33). Gemsbok males appeared to associate with greener grass and greener ephemeral dicot conditions than the females.

DISCUSSION

It is apparent that gemsbok and wildebeest differed greatly in their range use patterns, irrespective of their similar grass and roughage feeding habits and similar body masses. Although the ranges of most individuals continued to increase over time, even after extended periods of monitoring, the many significant differences in range sizes between species, sexes, years, seasons and lumped rainfall periods (drought and post-drought) presents valid variations, although they may underestimate the actual ranges.

The gemsbok data presented are comparable with that found for the oryx of East Africa (Western 1975, Wacher 1986), that also predominantly display the 'resident' movement patterns, of fairly stable ranges further from waterholes than the more drinking-water dependent wildebeest. However, the presence of available water did influence the ranging behaviour of gemsbok, as was particularly evident amongst those females resident in the waterless GNP, whose ranges shifted westwards towards the water supplies in the dry season. On the otherhand, male movements appeared relatively uninfluenced by water supply. Similar responses to available water in the dry seasons were noted for gemsbok in the Namib Desert (Kok pers comm. [2]), Etosha National Park (Du Preez & Grobler 1977, Berry 1982) and fringe-eared oryx at Galana ranch (Wacher 1986).

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All but one of the radio-collared wildebeest failed to show any 'migratory' tendency and their movements can be described better as a restricted 'dispersal' system of wet season scattering and dry season concentrations, predominantly around fresh waterholes distributed along the Nossob and Auob riverbeds. The 'restricted' qualification rises from the lack of definite dry and wet season ranges as exist in typical dispersal systems such as in Amboseli (Western 1975) and Tarangire (Talbot & Talbot 1963). Besides the overall increase in wet season ranges, indicative of dispersal, the season was also characterised by infrequent and uncoordinated long range movements by groups of mixed wildebeest herds. The occurrence of two aseasonal treks away from drinking water by wildebeest females WO3 and WO1 in April to May 1985 and October 1985, respectively, probably resulted from the drought conditions that prevailed at the time. However, with above average rainfall, as occurred in 1988 and 1989, wildebeest were able to remain in the GNP on a more permanent basis without drinking water as was found for wildebeest female W24, during 1989. After her capture in March of the same year and with the onset of the dry season she slowly and progressively drifted to the north-east up the rainfall gradient in the typical manner described for the migratory populations in the Serengeti (Maddock 1979). In fact for the first time in five years small wildebeest groups were noted in the GNP and the adjoining northern WMA area during the July 1989 aerial survey, when an estimated 1782±1648 (±SE) wildebeest were seen in the region (Knight 1990). Ngwamotsoko (1985) speculated from analysis of aerial census data from the western Central Kalahari, that wildebeest periodically commuted between the southern Kalahari and his survey region to the north where larger wildebeest populations usually occurred.

Rainfall played an important role in annual and seasonal range use by both species, as a direct result of increasing availability of both good quality vegetation (Chapter 3, Coe et al. 1976, Seely 1978) and surface drinking water (Maddock 1979). Although no significant correlation was detected between annual range sizes and rainfall variables, probably owing to limited sample sizes and large individual variations, a trend in decreasing range sizes with increasing

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rainfall (over years and between the drought and post drought periods) was evident for both gemsbok and wildebeest females. Females of most African ungulates directly reflect nutritional requirements while those of the males are restricted by social pressures (Owen-Smith 1988).

Besides rainfall, the easy access to permanent drinking water resulted in further reductions in range sizes as evident between the gemsbok females resident in the KGNP and waterless GNP. The presence of permanent drinking water also appeared to buffer the differences in annual ranges between populations with different rainfall regimes, as the average annual range size of 314±96 (±SD) km^2 for gemsbok females resident in the KGNP during the post-drought, exceeded the average 219 km^2 for fringe-eared oryx on Galana Ranch (Wacher 1988), where the annual rainfall averaged 400-800 mm in comparison to the 220 mm in the KGNP. However, the 10 fold difference between the 2000±1015 km^2 annual ranges in the GNP and 50-212 km^2 in the central Kalahari where annual rainfall averaged a higher 350 mm (Williamson & Williamson 1988) and where also no permanent drinking water exists, emphasises not only the magnitude of difference in range size in the lower rainfall regions owing to the wide variation in the relationship between rainfall and primary production (Seely 1978), but also the potential differences between habitats and regions. This point is further emphasised by interspecific comparisons of annual ranges against body masses, as the annual range estimates of gemsbok in the KGNP and GNP in the post-drought period were 30 and 200 times greater respectively, than the ranges predicted from body mass (Owen-Smith 1988). Ranges noted in the drought periods were a further 50 and 400 times greater respectively, than predicted. Most of Owen-Smith's (1988) information used in calculating the home range-body mass relationship were drawn from species occupying mesic environments which suggests it has little relevance to ungulates inhabiting arid areas, or where water is not provided.

With the exception of Amboseli (Western 1975), little information exists on the movement patterns of more resident wildebeest populations in semi-arid areas,

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as wildebeest predominantly resort to migratory behaviour to exploit drier regions in the wet season (Pennycuick 1975, Williamson et al. 1988). Therefore, the artificial situation that exists with respect to the wildebeest in the KGNP and other areas, like Etosha (Berry 1982) where water is provided and migration routes are blocked, populations remain permanently in their historic summer grazing areas. Thus, the situation exists where the now resident wildebeest attempt to make the best of potentially adverse circumstances, where owing to the low average rainfall and poor predictability (Tyson 1986), suitable grazing conditions are highly variable in time and space. Furthermore, wildebeest are selective for grass leaf and sheath (Gwynne & Bell 1968, Owaga 1975, Berry & Louw 1982c) and owing to their mouth structure (see Chapter 3, Bell 1971, Owen-Smith 1982), they are restricted to grazing short grass communities, such as occur on the periphery of the pans and dry riverbeds in the Kalahari, which make up less than 5% of the region. These habitats were positively selected for in all seasons in the drought and post-drought periods. In addition, the wildebeests relatively higher water demands owing to their notably inefficient kidney in concentrating urine (Berry 1982), and high rates of evaporative cooling (Taylor 1968), necessitate frequent drinking from fresh waterholes (Knight, Knight-Eloff & Bornmann 1988). This further restricted their foraging ranges in the dry season, as only 42% of the 41 boreholes along the Auob and Nossob riverbeds were considered fresh (Dreyer 1987).

A conflict situation therefore exists with the need to both forage further afield for better grazing and remain in close proximity to drinking water supplies. During the drought years (1985-1987) the apparent need for more grazing resulted in increased winter ranges. In fact in October 1986 a wildebeest male (W13) and female (W1) together commuted a 37 km round trip between Kwang waterhole and the S. obtusa grasslands near Langklaas waterhole every two days for a week. The male had deserted his territory 35 km to the south during this period to utilize the available grazing far to the north. In 1983 around lake Xau in the central Kalahari the situation was even worse as the wildebeest had to travel at least 50 km to water which resulted in a huge die-off (Williamson &

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Williamson 1985). The unsuitability of the southern Kalahari for permanent residence by wildebeest is also reflected in their poor population recruitment during below average rainfall years (see Chapter 7) and their unusually long feeding periods (Chapter 5).

It has also been hypothesised that migration is a means of escaping predation by predominantly sedentary predators such as lions and spotted hyaenas (Fryxell et al. 1988). Although wildebeest constituted only about 4,0% of the large herbivore biomass (eland, gemsbok, wildebeest, red hartebeest and ostrich) (Knight 1990), they feature predominantly in the diet of lions and hyaenas, as Mills (1984) found 37% and 29% of lion and spotted hyaenas' kills to be on wildebeest. The relatively high ratio of 0,02 predators per km^2 (from Mills 1984) in comparison to an average density of 0,06 wildebeest per km^2 in the KGNP was higher than any other ratios reported by Fryxell et al. (1988) which suggests a possible important role of predators on the sedentary wildebeest population in the southern Kalahari, in addition to the harsh and variable environmental conditions.

The overall smaller annual, seasonal and between drought and post-drought period movement ranges of gemsbok compared to those of wildebeest, reflects the greatter adaptability of the former to permanent residence in the semi-arid southern Kalahari. The gemboks' relatively narrow muzzle, and hence potentially greater ability to select amongst taller grass swards (See Chapter 3) and use of browse predominantly in winter results in their more catholic choice of habitats, with particularly preferences for the taller perennial grasslands. Their avoidance (similar to wildebeest) of the tree savanna habitat and particularly for the S. kalahariensis community, which forms extensive monospecific park-like stands, is understandable considering the noxious secretions of S. kalahariensis and hence its limited grazing potential (Müller 1984, Skarpe 1986). Furthermore, the well described adaptations to conserve water such as a reduced metabolism, adaptive heterothermy, deep and slow breathing (Taylor 1968, Taylor 1970a) in conjunction with overall reduced

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diurnal activity, extensive shade use (Chapter 5), excavation of the water-laden underground storage organs (Williamson 1987) and greater selection for greener conditions (owing to wider habitat use) during the dry seasons, all facilitate the gemsbok's ability to occupy relatively smaller ranges.

The lack of difference between the wildebeest sexes in selecting for greener grasses is understandable, considering their restriction to short grasslands near fresh water. But, as male gemsbok apparently have a greater association with overall greener grass conditions than females, this is less easy to understand, and, indeed, is contrary to that found by Wacher (1986). The difference may reflect the males choice of prime habitat as an added attraction factor for females.

The maintenance of territorial behaviour by radio-collared gemsbok males during the severe drought years of 1985 and 1986 (when annual rainfall averaged 114 mm), suggests that this was still a viable mating system under the rainfall experienced. However, this may have been facilitated by the presence of the permanent water supplies. With further declines in annual rainfall to below 100 mm, as occurs in the pro-Namib, the territorial system is abandoned and adult gemsbok males resort to following the wandering herds (Kilian pers comm. [3]) as hypothesised by Wacher (1988) and also evident in the Arabian oryx (Stanley-Price 1986).

The wide variation in male wildebeest territory sizes over the years probably emanates from the overall marginal habitat for wildebeest, plus the extensive movements of female herds up and down the riverbeds, thus leaving territorial males alone for extended periods.

In conclusion, the two species vary radically in their range use patterns owing to morphological, physiological and behavioural differences. Thus, the KGNP

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and GNP park complex as it stands is sufficiently large to maintain a large resident gemsbok population, but only a small permanent wildebeest population. It is suspected that even with the further introduction of permanent waterholes in the present waterless GNP, the wildebeest population will not increase appreciably owing to the lack of suitable habitat. Besides, to what extent the stabilization of once wider ranging populations of ungulates in their semi-arid natural summer grazing areas will contribute to veld degradation needs to be further monitored to prevent a repetition of a Sahel situation (Sinclair & Fryxell 1985).