CHAPTER 2

STUDY AREA AND METHODS

Study Area

The Kalahari includes the arid and semi-arid areas of the vast sheet of aeolic sand that covers most of the interior basin of the southern African subcontinent. This includes most of Botswana, north western South Africa and eastern Namibia. A virtually indiscernible rise in the land surface, known as the Bakalahari Schwelle divides the Kalahari into southern and central drainage regions (Leistner 1967). The central Kalahari is drained by the northwards running fossil Okwa river-bed which is now made up of a series of sandy depressions. Four predominantly dry riverbeds of the Auob, Nossob, Molopo and Kuruman drain the southern Kalahari southwards towards the Orange River (Fig. 1). These rivers only flow in exceptionally wet years. The Auob and Nossob rivers run through national parks, with the Nossob forming the boundary between the Kalahari Gemsbok (South Africa) (KGNP) and the adjacent Gemsbok (Botswana) (GNP) National Parks. Together they cover 36 190 km^2 but with the adjoining Botswanan Mabuasehube Game Reserve and Wildlife Management Areas (WMA), the conservation area amounts to 80 000 km^2, one of the largest in the world.

Only in the south-western section of the southern Kalahari is the sand thrown into a series of long, predominantly vegetated, parallel or seif dunes. About 30 km east of the Nossob river-bed in the GNP the dunes are replaced with gentle undulating country.

The southern Kalahari is semi-arid receiving irregular rainfall in summer and widely fluctuating ambient temperatures, both on a daily and seasonal basis. The long-term (1972-1989) mean precipitation in the KGNP was 225,1 ± 127,9 mm (±SD), with a coefficient of variation (CV) of 56,9%. The annual CV's

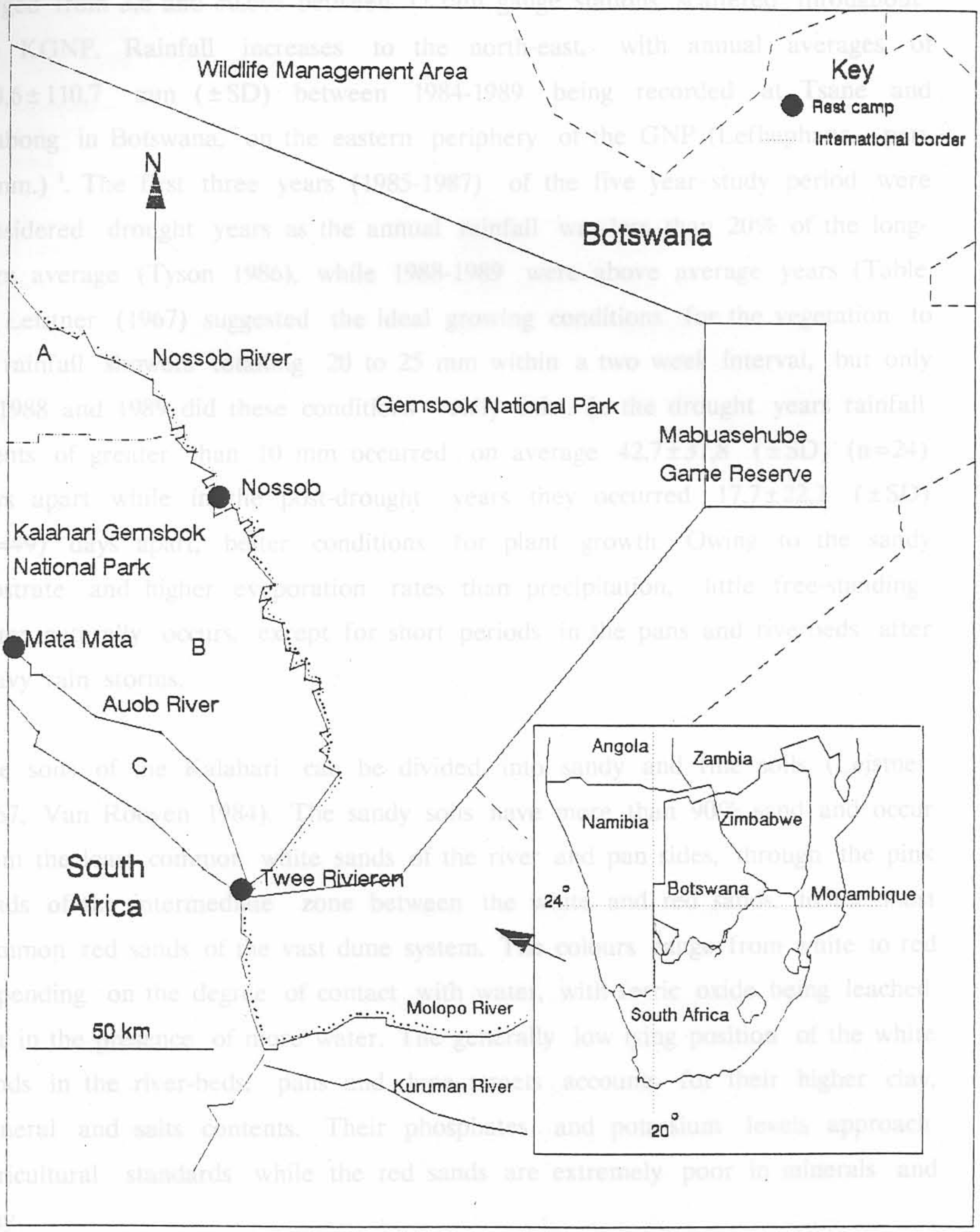

Fig. 1. The southern Kalahari, showing the Kalahari Gemsbok National Park, Gemsbok National Park and the surrounding Wildlife Management Areas. A, B, and C designates the three aerial census strata.

ranged from 3,6 and 50,6% between 11 rain gauge stations scattered throughout the KGNP. Rainfall increases to the north-east, with annual averages of 310,6±110,7 mm (±SD) between 1984-1989 being recorded at Tsane and Tsabong in Botswana, on the eastern periphery of the GNP (Lefhaphane, pers comm.) [1]. The first three years (1985-1987) of the five year study period were considered drought years as the annual rainfall was less than 20% of the long-term average (Tyson 1986), while 1988-1989 were above average years (Table 1). Leistner (1967) suggested the ideal growing conditions for the vegetation to be rainfall showers totalling 20 to 25 mm within a two week interval, but only in 1988 and 1989 did these conditions really exist. In the drought years rainfall events of greater than 10 mm occurred on average 42,7±37,8 (±SD) (n=24) days apart while in the post-drought years they occurred 17,7±22,2 (±SD) (n=49) days apart, better conditions for plant growth. Owing to the sandy substrate and higher evaporation rates than precipitation, little free-standing water naturally occurs, except for short periods in the pans and riverbeds after heavy rain storms.

The soils of the Kalahari can be divided into sandy and fine soils (Leistner 1967, Van Rooyen 1984). The sandy soils have more than 90% sand and occur from the least common white sands of the river and pan sides, through the pink sands of the intermediate zone between the white and red sands, to the most common red sands of the vast dune system. The colours range from white to red depending on the degree of contact with water, with ferric oxide being leached out in the presence of more water. The generally low lying position of the white sands in the river-beds, pans and dune streets accounts for their higher clay, mineral and salts contents. Their phosphates and potassium levels approach agricultural standards while the red sands are extremely poor in minerals and clay.

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[1] Mr A. Lefhaphane, Botswana Meteorological Services, Gaborone.

Table 1. Rainfall variables recorded at three stations in the KGNP between 1984 and 1989. Mean±SD.

Rainfall variables	Summer seasons				
	1984/85	1985/86	1986/87	1987/88	1988/89
Total (mm)	119±12	107±23	177±66	321±17	334±46
No. storms	22,8±1,5	26,3±3,1	26,0±10,1	36,0±9,5	40,7±11,9
No. storms ≥10 mm	3,3±1,5	3,3±1,5	4,3±1,5	9,3±1,5	9,0±1,0
No. days between storms	50,9±38,3	41,6±42,6	37,7±36,8	21,2±26,1	13,8±16,1
No. storms of ≥10 mm but ≤14 days apart	0,3±0,6	0,7±0,6	1,3±1,5	4,7±1,5	5,6±1,5

The fine sands of the riverbeds and pan surfaces have less than 90% sand with higher clay contents, and in contrast to the sandy soils, they have their origins in association with water. The mineral contents are generally higher than in the sandy soils but because of their higher clay contents they are poorly drained and water is lost via evaporation, which, particularly in the salt pans, encourages salt deposition in the upper levels. Grassy or incipient pans with a well developed herb layer occur in the absence of high salt depositions.

Acocks (1975) considered the vegetation of the southern Kalahari as a western form of the Kalahari thornveld, that is mostly an open shrub savanna with scattered trees, becoming increasingly more open down the rainfall gradient towards the south-west. More specifically the vegetation differs between sand types. The incipient pans, salt pan fringes and riverine habitats have short steppe-like grasslands with large Acacia erioloba and A. haematoxylon trees, while the dunes are more open with smaller A. erioloba, A. haematoxylon and Boscia albitrunca trees and a herb layer of tall perennial grasses. In the north-east of the GNP some broad leafed mainly deciduous woody species such as Terminalia sericea and Lonchocarpus nelsii also occur but deciduous, microphyllous species dominate generally (Skarpe 1986). The habitats and plant communities are described in more detail under the Movement Pattern methods section.

The southern Kalahari still has large populations of indigenous ungulates such as gemsbok O. gazella gazella, blue wildebeest C. taurinus, eland Taurotragus oryx, red hartebeest Alcelaphus buselaphus, springbok Antidorcas marsupialis, grey duiker Sylvicapra grimmii and steenbok Raphicerus campestris. The carnivores are represented by lions Panthera leo, leopards Panthera pardus, cheetahs Acinonyx jubatus, wild dogs Lycaon pictus, spotted hyaena Crocuta crocuta and brown hyaena Hyaena brunnea, but are predominantly restricted to the conservation areas.

Methods

Plant Production and Gemsbok and Wildebeest Feeding Ecology

1. Plant Productivity and Off-take

To monitor plant productivity, five sites were chosen in the Nossob camp area in the three most important habitats as follows: one site in the Panicum coloratum community in the river-bed; one in the Peliostomum leucorrhizum - Stipagrostis obtusa community of the flat riversides; and three in the Hirpicium echini-Centropodia glauca community of the red dunes.

At each site a 625 m^2 exclosure, effective against all large herbivores was erected in March 1986. Monitoring commenced immediately and was repeated on the following dates; May 1986, September 1986; February 1987; September 1987; March 1988; October 1988; April 1989 and October 1989. In October 1988, a further two exclosures were erected in each of the riverbed and flat riverside habitats.

Within all exclosures, at the first monitoring session, 10 1 m² wire quadrants were systematically laid down and their positions noted. In each quadrant the basal leaf and infloresence heights of the tallest representative of each grass species were recorded. Just above ground level the grasses and forbs were separately clipped and weighed. Samples were later dried to constant mass in a drying oven set at 60° C.

Outside the exclosures 20 1 m² quadrants were selected by a random toss over one's shoulder. The grasses and forbs were similarly processed and harvested as mentioned above to determine outside standing crops. In each subsequent collection period a different direction away from the exclosure was chosen to reduce successive sampling of the same area.

During subsequent sampling within the exclosures the quadrants previously clipped were reclipped to monitor productivity over the elapsed time period and determine the annual aboveground net primary productivity (ANPP). A further 10 systematically placed quadrants were laid down in an adjacent unclipped area of the exclosure and monitored as above.

At each site a rain gauge was installed and regularly monitored. Oil was placed in the gauge to prevent evaporation.

In addition to the above sites a further four study sites without exclosures were established in March 1986 in the vicinity of the hypersaline Kousaunt and Langklaas waterholes 50 km further up the Nossob river-bed. At each of these sites 20 quadrants of 1 m² were selected randomly and analysed in the same manner as for the exclosures.

At each site single weighed samples of the major grasses, forbs, and woody plants such as A. erioloba, A. haematoxylon, A. mellifera and Grewia flava were taken, and later oven-dried at 60°C to obtain moisture content.

On a monthly basis from September 1988 until August 1989, three samples of the grasses Stipagrostis obtusa, Eragrostis lehmanniana and Schmidtia kalaharensis (clipped just above ground level) and terminal leaf bunches, including twigs, of three woody species A. erioloba, A. haematoxylon and G. flava were collected shortly after sunrise and oven dried at 60° C to constant weight to obtain water content. In addition, 0,5 g samples of the dried and ground samples were analysed for protein content by the Kjeldahl method (Horwitz 1970) and for NDF (neutral detergent fibre) by the method of Van Soest (1964) using a Fibre-Tec 1020 hot extraction unit.

Simultaneously from the same vicinity, four soil samples were collected in air tight bottles at 30 and 50 cm below the surface from the red sand dunes and white sands of the riverside.

2. Tsama Melon Counts

Monthly from July 1988 to April 1989 counts of Tsama melons Citrillus lanatus were made in two areas, one near (3 km) and another far (17 km) from fresh sources of water. At the 'near' site three transects of about 480 m long subdivided into three roughly equal length sections were marked with poles. At the 'far' site three transects of 240 m long, subdivided into two sections were also marked permanently with poles. All tsama melons lying within 1,5 m of each side of the transect line were recorded, noting if they were whole (ie. uneaten) or eaten.

3. Feeding Behaviour

Once a month from April 1988 to July 1988, and thereafter twice a month to May 1989, radio-collared representatives of both gemsbok and wildebeest were located in the late afternoon. The following morning their tracks were followed and feeding records documented following the 'plant based acceptance' method of Owen-Smith & Cooper (1987). The first feeding site, defined as the first evidence of feeding seen directly along the animal track, was noted for: a.) plant species, b.) greenness (1-5 scale of brown to green), c.) grazing height (cm); d.) basal leaf height (cm) (only for grasses), and f.) inflorescence height (cm). Within 1m of the feeding site, the number of other plant species occurring, their greenness and whether eaten or not was recorded. The next feeding site selected was taken as the fifth one seen down the animals track to reduce overlap of the one metre feeding circles. If the feeding circle came within two metres of another animal's tracks the next station was taken, but fortunately animals rarely foraged within six metres of each other.

A minimum of 50 feeding sites were sampled per session. The group of animals was then tracked until located to obtain their nocturnal foraging distances.

A single diet sample was collected early the next morning in the same proportions, with respect to species and quality, as eaten by gemsbok and wildebeest. Grasses were clipped just above ground level and the browse was hand plucked, thus including leaves and terminal stalks. Samples were oven-dried to obtain water content and analysed for protein and fibre.

For diet overlap the 'similarity index' (S) (Odum 1971) was used:

$S=2C/(A+B)$ where A=the number of species in sample A, B=the number of species in sample B and C=the number of species common to both samples.

4. Statistical Analyses

Productivity, standing crop, grass height and bite height data were initially tested for normality (SAS 1986). Normal data were tested for significance using Student's-t and paired Student's-t tests. Non-normal data were log transformed before being subjected to the above tests.

Least squares linear regression was used for correlation analyses using SAS (1986). Comparison between regression coefficients were done according to Zar (1984).

Differential use of plant species and quality by the two ungulate species were tested using X^2 contingency tables. Confidence limits for species and plant quality selection were determined using the method of Neu, Byers & Peek (1974).

Movement Patterns

This aspect of the study extended from October 1984 to November 1989.

1. Animal Marking

Animals were darted and captured using 'Fauncap' darts fired from a 'Capchur' immobilizing rifle from either a helicopter or a vehicle. A drug mixture of M99 (etorphine hydrochloride, Reckitt and Colman, Durban, South Africa) (3,5 mg and 3,0 mg for adult gemsbok and wildebeest respectively) and Rompun (xylazine, Bayer) (15 mg and 30 mg for adult gemsbok and wildebeest respectively) was used to immobilize animals.

Animals were equipped with radio collar types MOD 500 or 600 (Telonics, Mesa, USA) which weighed on average 600 g and operated in the 148-149 MHz range with an approximate battery life of three years. A portable TR-2/TS-1 radio-receiver/scanner combination (Telonics, Mesa, USA) with either hand-held RA-2A (Telonics, USA) or vehicle-mounted RA-4A (Telonics, USA) were used for radio-locations on the ground. The same radio-receiver/scanner and two RA-2A antennae attached to the struts of a Cessna 182P were used to locate animals from the air.

2. Locations and Habitats

With every fix the following variables were recorded:

1. Date.
2. Group characteristics: total number; number of adults and juveniles.
3. Position:

A. Ground based. Fixes were ascertained by noting the compass bearing and distances driven (as indicated by the vehicle odometer) from known positions.

B. Aerial based. For every fix less than 5,0 km from a known position, the distance was estimated, and the bearing was recorded from the aircraft's compass by aligning the aircraft with the known position. For fixes further afield, positions were determined from bearings (from aircraft compass), flying time and air-speed to known positions. All positions were noted in Universal Transverse Mercator (UTM) coordinates.

4. Habitat. Six habitats based on physiognomic characteristics were used following Van der Walt, Retief, Le Riche, Mills & De Graaf (1984).

A. Tree savanna: A prominent tree stratum averaging some five metres in height that includes A. erioloba, T. sericea and B. albitrunca, with a tall shrub layer dominated by the palatable G. flava. The presence of not more than 200 individuals/ha in the tree and shrub layer leads to a scattered grass/dwarf shrub layer and an extensively developed annual layer dominated by stoloniferous plants. Such grasses as Schmidtia kalaharensis and Schmidtia pappophoroides are common in the herb layer.

B. Dunes with A. haematoxylon: This is an extensive habitat with predominantly low rolling dunes with tall shrubs dominated by A.

haematoxylon, that attain their highest densities. The herbaceous layer is dominated by perennial grasses such as E. lehmanniana and C. glauca, annuals are thus of lesser importance.

C. Dunes with B. albitrunca: Similar to the above mentioned habitat, but with denser stands of B. albitrunca.

D. Plains: This area has a slightly undulating topography with A. haematoxylon dominating the shrub layer. B. albitrunca is conspicuously absent. The herbaceous layer consists predominantly of the perennial grass E. lehmanniana, C. glauca and Stipagrostis amabilis.

E. Rivers: Includes the Nossob and Auob fossil riverbeds that are further subdivided as follows :

a.) River-bed: Alluvial soils with high clay or silt contents dominated in places by P. coloratum and tall A. erioloba and A. haematoxylon.

b.) Flat riversides: Slightly elevated but compacted soils deposited by fluvial action. The perennial S. obtusa, dominates the herbaceous layer in places, with small shrubs consisting predominantly of P. leucorrhizum and Rhigozum trichotomum, with the latter becoming dominant in areas.

c.) Calcareous riversides: Found on fairly solid calcrete exposures. It consists predominantly of the shrub R. trichotomum, with the herbaceous layer consisting of S. obtusa and the annual grass Enneapogon desvauxii. Dwarf shrubs such as Aizoon schellenbergii and Zygophyllum pubescens are characteristic of this habitat.

d.) Dune-sides: Normally high dunes with a predominantly pink colour. The tree and tall shrub layer are of lesser importance than in the tree savanna and river-bed habitats, while the grass/dwarf shrub layer is better represented. The shrubs consist mainly of A. mellifera and R. trichotomum, while the perennial grass Stipagrostis ciliata features amongst the herbaceous layer.

F. Pans: These are shallow depressions with a flat, often level surface with internal drainage. The typical pan has a hard, naked flat floor of very compact and almost impervious clayey soils with a higher pH and mineral contents than the surrounding dunes (Leistner 1967). On the pan itself little grows except an annual grass Sporobolus coromandelianus. The flat floor is surrounded by vegetational communities largely by dominant dwarf shrubs, similar to that found on the riversides (Leistner & Werger 1973).

G. Sand pans or 'braks': Incipient pans or pans being smothered by encrouching sand. These are generally shallow depressions in dune streets, lined with fairly compact, white calcareous sand (Leistner & Werger 1973). They lack trees and tall shrubs having mainly dwarf shrubs such as Monechma incanum, with the perennial grass S. ciliata in association.

5. Community: Thirteen communities were identified following Leistner & Werger (1973) and Skarpe (1986). Variations in the vegetation was found to correlate with soil types of which two types, sandy and fine soils (Leistner 1967) occur.

A. Communities of sandy soils

Three categories exist ranging from red, through pink and white soils, depending upon the extent to which ferric oxide coats the grains (Leistner 1967). As sand covers at least 90 % of the surface of the southern Kalahari, its communities are by far more extensive than those of the finer soils.

a.) Stipagrostis amabilis type: This typically open community on the sands with the character species of S. amabilis and Eragrostis trichophora occurs on most dune crests of the Kalahari Gemsbok National Park (KGNP) and on the undulating to almost level plains between the Nossob and Auob riverbeds. The tree and shrub layer is formed by A. haematoxylon, A. erioloba and B. albitrunca.

b.) Stipagrostis amabilis--Terminalia sericea type: With higher rainfall in the northern reaches of the KGNP the woody taxa include other species such as T. sericea and Rhus tenuinervis in addition to those of the above community.

c.) Hirpicio echini--Centropodia glauca type: This community associates with red sand dunes streets or valleys and on the lower slopes of dunes. The tree or shrub element seldom exceeds 1,5 m, with the most common species including A. haematoxylon, G. flava and A. erioloba. Character species include the important perennial grass C. glauca, as well as Stipagrostis uniplumis. The perennial herb Acanthosicyos naudinianus, the gemsbok cucumber, important as a source of food and water for animals, often have their highest abundance levels in this community.

d.) Schmidtia kalahariensis type: This community occurs over vast expanses of the southern and central Kalahari, on pink, fairly compact sand. It frequently takes on a parkland appearance with large trees, mostly A. erioloba, a shrub layer of A. mellifera and G. flava, with the herb layer dominated by S. kalahariensis.

e.) Schmidtia pappophoroides--Stipagrostis uniplumis type: Found predominantly on red sand on undulating or low dunes and often forms an open shrub savanna with a few A. erioloba, A. luederitzii and B. albitrunca trees. Shrubs include A. mellifera and G. flava with the herb layer dominated by the perennial grass S. pappophoroides and S. uniplumis, with E. lehmanniana also common.

f.) Monechma incanum--Stipagrostis ciliata (Sandpans or 'braks') type: This community occurs on pink shallow sands that cover an underlying calcrete sheet or sand pans or dune streets that experience internal drainage. No trees or large shrubs occur and species dominating include the dwarf shrub M. incana and perennial grass S. ciliata.

g.) Monechma incanum--Stipagrostis ciliata (river dunes) type: Occurring on the pink dunes along the Nossob and Auob riverbeds, the community differs from the above in having tree sand shrubs present, such as A. mellifera, A. erioloba, G. flava and B. albitrunca.

h.) Aizoon shellenbergii--Indigofera auricoma type: This community occurs on calcrete exposures with predominantly white sand, and correlates with that described for the calcareous riverside habitat.

B. Communities of the fine soils.

These include those of the pans and riverbeds.

a.) Sporobulus lampranthi--Zygophyllum tenue type: Occurs on pan-like slightly elevated alluvial flats of the Nossob river-bed. It is an open community dominated by the darkish dwarf shrub Zygophyllum tenue, with the dwarf shrub Salsola rabieana also common. Grasses consist of Sporobulus lanpranthus and Eragrostis truncata.

b.) Sporobolus coromandelianus type: This community has no perennial plant cover and occurs on soils with a high mineral and clay content on the flat pan surface. The annual grass S. coromandelianus usually accompanied with the annual succulent Trianthema triqueta occur after rains.

c.) Sporobulus rangei type: This community occurs, where thin layers of white calcareous sand accumulates on the pan surface or intermediate periphery, and is characterised by S. rangei, with the low tufted grass E. desvauxi also present.

d.) Peliostomum leucorrhizum-Stipagrostis obtusa type: Occurs on white compact sand deposited by both aeolian and fluvial action on the riversides and pan fringes. Character species consist of P. leucorrhizum, R. trichotomum and the abundant perennial grass S. obtusa. Trees are rare and consist of A.erioloba and A.haematoxylon that grow between 4-8 m.

e.) Panicum coloratum type: This community correlates with the riverbed habitat. The development of this community is dependant upon soil moisture where water penetrates to 2,0 m or more, pure stands of P. coloratum, with Chloris virgata in association occur. With waterlogging, stands of the tufted perennial grass, Eragrostis bicolor may occur. Where moisture penetration is less deep or less uniform or where grass cover has been damaged or destroyed, herbs predominate, such as the unpalatable Geigeria pectida, Stachys spanthulata and Galenia africana.

6. General veld condition.

The following subjective codes for general condition were given:

A. Overall grey-brown colour, with little to no greenness.

B. Definite green tint among old grey-brown old growth.

C. Verdant bluish green.

7. Grass condition:

Arbitrary codes were given for subjective assessments of greenness, height and phenology (Table 2) and for density (Table 3). Density estimates for the grass were estimated according to the comparative yield method (Haydock & Shaw 1975).

8. Annual condition:

Similar arbitrary codes were given for greenness (Table 2) and density (Table 3) as mentioned above.

9. Browse condition:

Similar codes for greenness (Table 2) were used, while the density of browse was estimated from the number of plants per $100m^2$ plots (Table 3).

10. Signs of burning:

A. No sign

B. Burnt last summer

C. Burnt this summer

Table 2. Subjective codes used to classify the degree of greenness, density, height and phenology of grass.

Code	Greenness	Height	Phenology
1	25%	tall (>40cm)	sprouting
2	50%	short (<40cm)	short (<12cm)
3	75%		intermediate, no flowers
4	fully green		mature, flowers present
5			moribund
6			dormant
8	brown		
9	zero	zero	zero
0	?	?	?

In an attempt to record available habitats and their conditions while tracking from the air, the above veld condition assessments were noted approximately every three minutes irrespective of direction of flight.

Table 3. Subjective codes used to estimate density of grass (g/m^2), ephemeral dicots (g/m^2) and woody plants (number of plants/100 m^2).

Plant group	Habitat	Codes			
		1	2	3	9
Grass	Dunes	<40	41-100	>100	0
	River-bed	<10	11-100	>100	0
	Riverside	<5	6-20	>20	0
Dicots	Dune	<5	6-10	>10	0
	River-bed	<10	11-20	>20	0
	Riverside	<10	11-20	>20	0
Woody plants	Dune	<2	2-3	>3	0
	Riverside	<4	4-28	>28	0

3. Data Analyses

Both annual and seasonal home ranges were estimated by the convex polygon method (MAM) (Mohr 1947) and the Jennrich & Turner (1969) 95% ellipse method using the programme MCPAAL (National Zoological Park, Smithsonian Institute, Front Royal, USA). Owing to the expansive study area, a minimum of seven and 10 locations were considered sufficient in estimating their range use per season and year respectively. For the analysis of the home range data the year was defined as extending from the beginning of one summer to the next ie. November to October and divided into two seasons, summer (November to April) and winter (May to October). Otherwise three seasons were considered: the hot-wet (HW) season, January to April; the cold-dry (CD) season, May to August; the hot-dry (HD) season, September to December (Mills & Retief 1984a). Drought and post-drought years extended from 1985-1987 and 1988-1989 respectively.

The accuracy of radio-tracking locations were tested by comparing the estimated position of a radio-collar (on either a dead animal or one that was broken off through fighting) against the actual position determined on the ground from a compass bearing and vehicle's odometer reading from a known feature.

Home range, distances between locations and distances from waterholes data were initially tested for normality. Non-normal data were log transformed and then subjected to ANOVA and GLM (general linear models) for analysis of variance (SAS 1986). Significances between means were tested with Student's-t tests. Pair-wise analyses were done using Wilcoxon matched pairs (T) (Siegel 1956) and paired Student's-t tests (SAS 1986).

Correlation analyses for ranked and unranked data were done using Spearmans rank (r_s) (Siegel 1956) and least squares linear methods, respectively (SAS 1986).

Distances between subsequent fixes for each animal were corrected for the number of days between sightings.

Available habitats in the KGNP were calculated by cutting and weighing each habitat from a habitat map developed by Bothma & De Graaf (1973). This was pooled with the percentage habitat availability in the GNP which was estimated from habitat information systematically collected every three minutes during two aerial surveys undertaken during 1989. The frequency of occurrence of the 12 communities available in the KGNP and GNP were similarly estimated from three and two aerial surveys undertaken in each park, respectively. Differential habitat utilization for both species by season and year was determined using χ^2 contingency tables from pooled radio-tracking observations. Habitat preferences were calculated using the Bonferroni z statistic (Neu et al. 1974).

Behavioural Observations

1. Diurnal Activity

Diurnal activity of both gemsbok and wildebeest was followed from sunrise to sunset, for two days per month on mixed herds from September 1986 to August 1987. All observations were made from a vehicle 50 m to 400 m from the herd.

The five-minute interval instantaneous scan sampling (Lehner 1979) procedure was adopted to record the activity of adult individuals. The behavioural categories recognised were: feeding (standing or moving), moving (either walk or run), resting (either standing or lying), social and other. The numbers of animals performing each activity in the shade of trees were also noted.

Once every 20 min the numbers of animals orientated differently to the sun and prevailing wind were noted. Five positions in relation to the sun and wind were recorded: head directly towards; head angled 45° away from; lateral; rump angled 45° towards; rump directly towards the sun or wind.

The same habitat variables, described in the **Movement Pattern** section above, were recorded approximately every half hour or when changes occurred through animal movement. Additional variables noted were the sand colour (red, pink or white), and section of dune used (crest, side or valley).

Environment variables noted on a half-hourly basis or when changes occurred were: cloud cover (0-5 scale); wind speed (measured in m/sec with a Wind Wizard speed indicator); ambient shade temperature; and 'black'-bulb temperature (measured with a standard thermometer set in a table-tennis ball painted matt black).

Initially data were recorded directly onto a dictaphone and later transcribed onto data sheets. In the latter half of the study, data were recorded on a Psion Organiser II data capture unit, which was down-loaded onto an IBM AT personal computer.

2. Nearest neighbour distances

Three distance estimates of nearest neighbours were noted approximately every 30 min during the diurnal behavioural observations. From a radio-collared or easily identifiable animal (A) within the study herd, the distance (in m) to its nearest adult neighbour (B), and inturn the distance to its nearest neighbour (C), and its distance to its nearest neighbour (D) were noted. If two animals were touching they were recorded as one metre apart.

3. Nocturnal activity

The nocturnal activity was estimated through monitoring the frequency of occurrence of two activities 'active' and 'stationary' as determined by the pitch modulation of incoming radio signals from radio-collared animals. Once a month from August 1986 to September 1987 (except for February and March 1987), from a high point in the vicinity of radio-collared gemsbok and wildebeest, each animal was recorded as being either active or stationary every 10 min from sunset to sunrise.

In an attempt to correlate the pitch modulation with actual activity, radio-collared animals in the diurnally observed groups for both species were listened to and classified as either active or stationary, and their behaviour recorded.

4. Statistical Analyses

Frequency data were initially arcsine transformed (Sokal & Rohlf 1982) before significances were tested with ANOVA (SAS 1986) and non-parametric tests such as Mann-Whitney (U) and the Wilcoxon matched-pairs (T) (Siegel 1956).

Correlations were tested using least square linear analysis (SAS 1986).

Use of Boreholes and Lick Sites

1. Observations

Single 24 h observation sessions were undertaken monthly over the full moon period at the fresh (<5000 parts per million (ppm) total dissolved solids (TDS) as defined by Boocock & Van Straten (1962)) Cubitje Quap (CQ) and the hypersaline (>10000 ppm TDS) Kousaunt (KN) waterholes, that were 44 km apart on the dry Nossob river. Observations were undertaken from March 1984 to April 1985.

The instantaneous scan method (Lehner 1979) with a five minute interval was used, recording the numbers of gemsbok and wildebeest, and other ungulates such as steenbok, springbok and red hartebeest within 50 m of the waterhole. The numbers drinking, practising geophagia and other activities (lumped into a single category) were noted, in addition to the numbers that drank from the storage tank, overflow or trough. Observations were made from a vehicle situated within 300 m of the waterhole in the day and 100 m at night. Rainfall during the study period was monitored monthly from Nossob (NS) and Groot Brak (GB), that were within 10 km of CQ and KN respectively.

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

Selection for habitats on white (including riverine soils) and red sand habitats by the ungulate species were determined from radio-collared animals. All radio-collared animals (11 gemsbok, 10 wildebeest, three red hartebeest and five springbok) were located once every 2-3 weeks over the study period and the sand types and habitats on which they occurred were noted. Steenbok habitat use on white or red sands was extracted from monthly ground counts (n=10) undertaken along the same routes along the Nossob and Auob riverbeds (422 km) and within the dunes (247 km) using the same methods mentioned above.

2. Water analyses

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

3. Soil analyses

Soil samples were collected from actively used lick sites near the two water-holes. Non-lick soil samples were taken randomly from the surrounding soil at the same depth as at the exposed lick sites, but from at least 5 m away.

Extracts of saturated pastes of the samples (Buys 1980) were analysed for: potassium, calcium, magnesium, sulphate, chloride and carbonate ions, pH and conductivity. Phosphorus was extracted according to the Bray no.2 method (Bray & Kartz 1945).

4. Statistical Analyses

Interval data were initially tested for normality (SAS 1986). Significant differences between means for normally distributed data were tested using the Student's-t test. For non-parametric data the Mann-Whitney (U), Wilcoxon matched pairs (T) and Sign tests were employed (Siegel 1956).

Percentile data were initially arcsine transformed (Sokal & Rohlf 1982) before being tested with the χ^2 contingency tables (SAS 1986).

Regression equations were calculated by the method of least squares (SAS 1986).

Population Dynamics

1. Ground Counts

Once every two to three months counts were made along the same route in the Nossob and Auob riverbeds (422 km) and within the dunes (247 km). The following variables were noted for gemsbok and wildebeest:

A. Number and group size: All individuals seen were counted and the size of groups noted. Gemsbok individuals within 100 m of the largest concentration of individuals were considered inclusive of the group, while within 50 m was considered inclusive for wildebeest. The arithmetic mean and typical group sizes were both calculated (Jarman 1974), where the latter of which better represents what the average individual experiences..

B. Age and sex structure: For gemsbok the age classifications recognised by Dieckmann (1980) were used with: 1) 0-2 months, 2) 2-4 months, 3) 4-6 months, 4) 6-10 months, 5) 10-17 months, 6) older than 17 months. Calves were lumped to include individuals < 10 months, with yearlings equal to the 10-17 month class, and adults were considered older than 17 months. Sexing was attempted on all adults and sub-adults using the presence/absence of penal sheaths (easily seen in males), and the thickness and length of horns (with males having shorter, thicker horns than adult females). Sexes of calves were determined opportunistically when clearly visible.

Sex ratios were determined in two ways. 1) The total estimated sex ratio from all observations made during a counting session irrespective if all group members were seen or not, and 2) a more specific estimate of sex ratios of gemsbok mixed groups larger than 10 individuals that were further subdivided into those with (AWJ = adults with juveniles) or without (ANJ = adults and no juveniles) juveniles (less than 10 months of age) following Wacher (1986).

Wildebeest were aged using Attwell's (1980) visual classes of : calves (< 1 year), subadults (2-3 years old), adults (> 3 years old). Sexes of adults were noted regularly, but those of subadults only when clearly visible.

C. Body condition: Subjective body condition indices with five classes: excellent, good, fair, poor and very poor for wildebeest (Berry & Louw 1982a) and gemsbok (Hamilton, Buskirk & Buskirk 1977) were used to assess the individual conditions in every count. Visual condition was based upon skeletal details visible, such as the extent to which the ribs and hips protruded and the roundness of the hindquarters.

2. Aerial counts

Biannual aerial surveys were conducted during the transitional period between summer and winter (April-June) and winter and summer (September to December) from 1984-1989.

The KGNP was subdivided into three strata (Fig. 1). Stratum A was restricted to the northern savanna woodland area of the park, with its northern boundary demarcated by the upper reaches of the Nossob riverbed. The southern boundary extended east-west through the Kraalpan area to near Langklaas waterhole on the Nossob riverbed. Stratum B extended south to the Auob riverbed and covered the central grasslands. Stratum C extended south of the Auob to the southern boundary fence. A total of 5, 10 and 8 systematically placed north-south transect lines were initially flown in strata A, B and C respectively. From 1986, the number of transects were increased to 7, 14 and 12 in each of the strata respectively.

Censuses were undertaken in a Cessna 206 with one observer on either side in the rear seats. The recorder was seated beside the pilot. The transects were flown at a height of 90 m (300 feet) maintained with the aid of a radar altimeter and at an airspeed of 90 mph. From 1985 to 1986 all animals seen within 500 m strips (demarcated by streamers attached to the struts, as described by Pennycuick & Western (1972)) were counted and recorded directly into a dictaphone. The species, adult and calf compositions, habitat and plant communities were noted with each sighting. At about three minute intervals the habitat and plant community directly below the recorder were also noted.

From October 1987 each strip was further subdivided into five strip width classes (0-100 m, 101-200 m, 201-300 m, 301-400 m, 401-500 m) with extra streamers. The strip width class in which the centre of each animal group occurred was recorded as were all animals seen outside the last strip.

Animal densities were calculated according to strip line theory using the ratio method (Caughley 1977) and line transect theory (Burnham, Anderson & Laake 1980). Comparative density estimates were made for strip sizes of 300 and 500 m. Incorporated into the ratio method calculations, correction factors for visibility biases between observers and distance from the aircraft were determined using the basic framework of the Petersen mark-recapture estimate (Seber 1982), in which animal numbers seen by the front observer/recorder on the right-hand side are said to be marked, and the number of those 'marked' that are seen and said to be 'captured' by the rear observer on the same side were noted. The mean correction factor (C) for both observers was calculated according to Marsh & Sinclair (1989) by :

$$C = ((Sf + b)(Sr + b))/(b(Sf + Sr + b))$$

where Sf = number of animals seen by the front observer

Sr = number of animals seen by the rear observer

b = number of animals seen by both observers.

The coefficient of variation (Cp) for the perception factor was calculated as:

$$Cp = ((Sf + Sr)/(Sf + Sr + b)^{*}\sqrt{(Sf^{*}Sr)/(b(Sf+b)(Sr+b))}$$

Noting animal sightings from each side of the aircraft separately allowed the calculation of a further correction factor for the influence of reduced visibility on the sunward side of the north-south orientated transects, assuming approximately equal animal numbers on each side.

A visibility correction factor for animals along line 0 (assumed to equate with the first 100 m strip) was incorporated into line transect calculations of density, using programme TRANSECT (Laake, Burnham & Andersen 1980).

Averaged correction factors for perception and side of aircraft were used in modifying previous surveys undertaken since 1974 (Mills, pers comm.) [2].

Numerical trends in populations numbers were measured by calculating the exponential rate of increase (r_{max}) derived by subtraction of the logged estimates of either one survey or annual mean from those of the previous survey or annual respectively, and standardised by month intervals between the two (Caughley, Bayliss & Giles 1984).

Seasons were divided into summer (November-April) and winter (May-October) categories, that were further subdivided into the hot-dry (HD) (September-December), hot-wet (HW) (January-April) and cold-dry (CD) (May-August) periods.

3. <u>Population Model</u>

Wildebeest calf survival rates were estimated using two methods. The first entailed calculating the differences between calf to adult female ratios, determined in game counts shortly after the January to February calving season and the last count of the year prior to the next calving season. The second method calculated the difference between expected natality (assumed to equal a pregnancy rate of 91,4 % for adult females (Attwell 1982)) and the calf to female ratio of the last count prior to the next calving season.

Gemsbok calf mortality rates were estimated as the difference between the expected natality (assumed to equal a pregnancy rate of 94,1 % for adult females (Mennie, pers comm.) [3] and mean calf to adult female ratios per year.

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Adult gemsbok and wildebeest survival rates were estimated through the multinominal method (White 1987) that grouped alive and dead collared animals (see Chapter 2) in proportion to the total number collared per year. A population model that incorporated three age classes; calves, yearlings and adults were used for both species. The yearling class consisted of two and three year-old animals. Three year-old 'yearling' gemsbok and wildebeest females were assumed to have a pregnancy rate of 51 % (Mennie, pers comm.) and 22 % (Attwell & Hanks 1980) respectively. Yearling mortality rates were assumed to be similar to those of adults, and adult males and females of both species were assumed to have similar mortality rates.

4. Statistical Analyses

ANOVA and GLM (general linear models) procedures were used for the analysis of variance of balanced and unbalanced normally distributed data sets respectively (SAS 1986). Significance between means was tested with Student's-t tests (SAS 1986). Non-normal interval data were transformed into common logarithms and tested as above. While, non-parametric data were tested for significance using the Mann-Whitney (U) and Wilcoxon matched pairs (T) tests (Siegel 1956). Percentile data were angularly transformed using the arcsine transformation (Sokal & Rohlf 1982) and tested with X^2 contingency tables (SAS 1986).

Least squares linear regression and polynominal regression were used for correlation analyses (SAS 1986).