Population Trends of Springbok (Antidocus marsupialis), Gemsbok (Oryx gazzella), and Wildebeest (Connochates taurinus) in Kgalagadi District, Botswana.

FREDERICK MBIGANYI DIPOTSO



# Population Trends of Springbok (*Antidocus marsupialis*), Gemsbok (*Oryx gazzella*), and Wildebeest (*Connochaetes taurinus*) in Kgalagadi District, Botswana.

# Frederick Mbiganyi Dipotso

# FMDIPOTSO@hotmail.com

A thesis submitted in partial fulfilment of the requirements for the award of a Master Degree in Tropical Ecology and Natural resources Management at the Norwegian University of Life Sciences (UMB) Ås Norway

> Department of Ecology and Natural Resources Management (INA) Universitetet for miljø-og biovitenskap

#### PREFACE

In recent years concerns have been raised over ungulate population decline, particularly Springbok (*Antidocus marsupialis*), in Kgalagadi District. Botswana's wildlife is of paramount national economic importance as the tourism sector, mainly because of wildlife, is the second revenue earner for the country's GDP after diamonds. With the country looking at the tourism sector for economic diversification, it is important for sound management practices to ensure sustainable viable wildlife populations. As a researcher in the Department of Wildlife and National Parks, Botswana, I found it important to conduct a research that will bring a better understanding of the population dynamics of ungulates in Kgalagadi and thus use adoptive management practices to halt or reduce population decline.

I will like to thank the Norwegian State Education loan bank, Lånekassen, for granting me a scholarship to pursue an MSc Degree. My gratitude also goes to the Botswana Ministry of Environment Wildlife and Tourism, and Department of Wildlife and National Parks for allowing me to go for my further studies I hope that my studies can contribute to a knowledge based wildlife management system in Botswana. I would like to thank the Department of Ecology and Natural Resource Management at UMB for accepting me in the department and for your financial assistance for my fieldwork.

For the individuals that assisted me, first of all I will like to thank research assistant Mmoloki Lepodise for your hard work in computerizing the data, without you I will not have made it. I will also like to thank Ronny Steen, Ellen Sanburg, for allowing me to walk into your offices unannounced and ask for your help. Stein R. Moe, my supervisor, I will also like to express my sincere gratitude to you for assistance on the thesis, knowing you as a person expecting quality work from your students I had to work harder and I hope I did not disappoint you. I am also indebted to my family especially my wife for taking care of our little girl and other things while I was gone you did a wonderful job. All my colleagues at work, thank you for the support you gave me during my field work, and studies.

# TABLE OF CONTENTS

PREFACE	2
TABLE OF CONTENTS	3
ABSTRACT	4
INTRODUCTION	5
METHODS	7
Study area	7
Data Collection	9
Data Analysis	11
Populations trends and distribution	11
Rainfall and populations	12
RESULTS	13
Population trends and distribution	13
Rainfall and populations	17
DISCUSSION	18
Population trends and distribution	18
Effect of rainfall	18
Effect of forage suitability	19
Effect of fire management practice	22
Effect of water provision	22
Rainfall and populations	23
CONCLUSION	24
ACKNOWLEDGEMENTS	26
REFERENCES	27

# ABSTRACT

Populations decline of many ungulates in south western Botswana, Kgalagadi, has been attributed to the erection of cordon fences in the 1980s which then resulted in massive die offs of migratory ungulates, especially wildebeest, during drought years. Human encroachment in Kgalagadi has pushed wildlife into marginal habitats, disrupting their migratory patterns through management activities and infrastructure development. One species that has had the largest population decline in the last two decades is the springbok. Springbok population development in Kgalagadi District was examined by accessing population trends and distribution. Dry season springbok population estimates from ten years of ground surveys in Kgalagadi Transfrontier Park (KTP) and nine years aerial surveys at district level were related to annual total rainfall, and other ungulates populations. Ground survey estimates showed significant decrease of springbok in KTP from 1998 to 2001, followed by no significant change in population. District estimates showed a decline in population of both springbok and wildebeest while gemsbok showed no change in population for both KTP and District estimates. Springbok population showed no significant correlation with rainfall and to other ungulates populations except with the wildebeest in KTP. Springbok population showed a significantly negative correlation to livestock population in Kgalagadi. Communal areas had the highest springbok density while gemsbok and wildebeest were more abundant in KTP than outside. This implies that KTP offers unfavourable condition for springbok, likely due to poor food quality as a result of lack of fire, and reduced larger herbivore populations in KTP. Food quality is likely the most determining factor in the population distribution and subsequently population dynamics of springbok in Kgalagadi. There is, however, need for information on the effect of fire on forage quality and resulting distribution and migratory pattern of springbok in Kgalagadi which could bring more light on the springbok population dynamics.

**Keywords:** Botswana, Kgalagadi District, Kgalagadi Transfrontier Park, population decline, springbok.

## INTRODUCTION

Wildlife population dynamics impacted by human encroachment is a cause of concern among conservationists (Sisk et al. 1994; MacDonald, 2003; Primack, 2006). Human population increase is often followed by an increase in demand for agriculture land and infrastructural development worldwide (Primack, 2006). These activities, in wildlife areas, often results in reduced populations, isolated small populations, and displacement of wildlife populations from their original habitats (Primack, 2006). Botswana's wildlife populations have not been spared by these challenges. The Kalahari, which is one of the last areas to be explored in Africa (Skarpe, 1986), stretches mainly from central Botswana to Namibia and north-western part of South Africa (Smithers, 1983). In Botswana the Kalahari, locally called Kgalagadi, had been inhabited by large numbers of animals which were mostly migratory, moving from Central Kalahari Game Reserve, through Wildlife Management Areas (WMAs), and communal lands to the Kgalagadi District in south-western arid part of the country, mainly to Kgalagadi Transfrontier Park (KTP) (Williamson & Mbano, 1988; Thouless, 1997). The migratory nature of the Kalahari ungulates makes them more vulnerable to habitat loss and habitat fragmentation as critical habitats are limited in the dry season, especially in the drought years (Spinage & Matlhare, 1992). Their ability to migrate long distances has been suggested to be of paramount importance in their survival (Parris & Child, 1973).

Kalahari was originally sparsely inhabited by humans because of its lack of surface water (Campbell, 1997). Ground water exploration by modern deep borehole drilling made it possible to keep livestock in Kalahari (Cooke, 1985; Arntzen & Veenendaal, 1986) transforming this arid area into one of the key beef producing areas for the country. Subsequently human population, infrastructural developments, and demand of land for cattle farming has increased in Kgalagadi. According to Campbell (1997) the human population was estimated to have increased four times and cattle by at least 10 times from the 1960s. The Increase in human population in Kgalagadi resulted in increasing wildlife habitat loss and fragmentation (Parris & child, 1968). Habitat loss and fragmentation are considered the major

threats to biodiversity worldwide (Primack, 1996). Infrastructure developments in Botswana such as veterinary cordon fences, cattle ranches, human settlements, and roads have disrupted many wildlife migratory routes, and have also displaced them to marginal habitats (Parris & child, 1968; Raborokgwe, 1997; Taolo, 1997). This has resulted in large numbers of die-offs during drought years when animals were trying to use the ancestral migratory routes to better pastures and water (Williamson & Williamson, 1984, Williamson, Williamson & Ngwamotsoko, 1988; Spinage, 1992). These barriers have also increased incidents of illegal off-take which can have substantial negative effects on wildlife populations (Newmark, 1996; Ngwamotsoko, 1997; Osborn & Parker, 2003).

In recent years populations of many wildlife species in Kalahari have been declining and one species that has been highly affected by this decline is the springbok (Skarpe, 1986; Spinage, 1992; Skinner & Moss, 2004; DWNP unpublished data). In Botswana the springbok is predominantly found in the Kalahari ecosystem ranging from Makgadikgadi-Nxai pan National Pak, central Botswana, to KTP. The stronghold of the population is reported to have been in Kgalagadi District, south-western Botswana (Bonifica, 1992b). Springbok populations has decreased across the Kalahari ecosystem from the 1940s in which single mass movements of as much as 50,000 animals where estimated (Child & Le Riche, 1969; Skinner, 1993). Aerial surveys from the 1990s estimated the country-wide population of over 100,000 springbok while recent Department of Wildlife and National Parks (DWNP) aerial surveys (2005) showed the country-wide springbok population to be 22,863 (8,085 SD). The change in the population from the 1990s to the present shows a great decline in the population of springbok in the last two decades. Several postulations of possible causal agents have been suggested (Williamson & Williamson, 1984; Mordi, 1989; Thouless, 1998; Bergström & Skarpe, 1999; Skinner & Moss, 2004) but none has been formally investigated. Aerial and ground survey data has been collected, this data, however, has not been compared with other possible agents of decline. There is no specific study that has attempted to find the causal agent of the springbok population decline in KTP and Kgalagadi District. It is hypothesised that springbok population decline in Kgalagadi is related to rainfall, larger

herbivore populations and increase in livestock numbers, and human activity. This Thesis examines population development of three ungulates in Kgalagadi, with special emphasis on springbok, by examining relationship between springbok population, and climatic data, livestock populations, and other ungulates (gemsbok and wildebeest) with which springbok is associated with (Skinner & Louw, 1996).

The objectives addressed in this thesis are therefore;

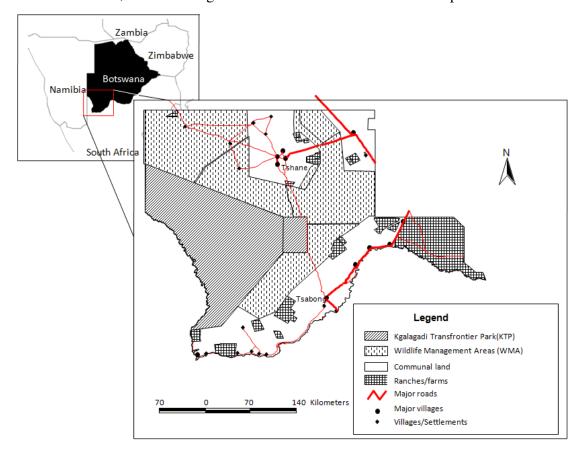
- 1. To determine population trends of the springbok, gemsbok and wildebeest,
- 2. To determine any relationship between climatic data, and wildlife populations, wildlife populations and livestock population, as well as relationship among wildlife populations, and
- 3. To assess management practices, in and around KTP, and their possible effects on the ungulate populations, and
- 4. To highlight possible areas of research for better understanding of the population decline and suggest management options that may help reverse or halt the decline of springbok.

## **METHODS**

# Study area.

The study was conducted in Kgalagadi District, in the arid Kalahari ecosystem in south-western part of Botswana, 20° 00'-23 ° 06' E; 23 ° 30'-26 ° 89' S (Fig 1). Ground counts were conducted in KTP only, while aerial surveys covered the entire district. KTP is a Transboundary conservation area comprising of about 28,400 km<sup>2</sup> of the former Gemsbok National Park in Botswana established in 1938, and 9,591 km<sup>2</sup> of the former Kalahari Gemsbok National Park in South Africa established in 1931. KTP on the South African side is fenced with a predator proof fence which extends into the southern side of the Park in Botswana for 120 km, separating the park with communal areas. The rest of the park in Botswana is then not fenced and surrounded by WMAs which are buffer zones between the park and communal areas. The section of the park in South Africa has numerous artificial waterholes established more than sixty years ago (Knight & Knight-Eloff, 1988). Nossob

valley, a dry river bed, forms the boundary between Botswana and South Africa and has become the most important area in terms of wildlife numbers throughout the year, mainly due to the establishment of artificial waterholes on the South African side of the park and along the river bed. WMAs hold substantial numbers of wildlife and some are important breeding areas for many ungulates (Williamson *et al.* 1988; Thouless, 1997) most likely owing to the numerous pans in these areas. There are some settlements in the WMAs that have recently expanded following their gazettement as villages. Though normally no activity is allowed in WMAs besides hunting during the safari controlled hunting season (May-September) cattle do enter WMAs, and the villages and settlements inside WMAs keep livestock.



**Figure 1.** Map of the study area, Kgalagadi District, with part of the District covered by Kgalagadi Transfrontier Park in south-western Botswana. (Modified from the Kgalagadi District Development Plan 6, 2007).

Kgalagadi District receives very little rainfall compared to the rest of the country with mean annual totals of 308.7 mm (136.3 SD) in the south (Tsabong) and 348.6 mm (137.0 SD) in the north (Tshane), for the past 38 years falling mainly from November to April (Department of Meteorology *unpublished data*). Temperatures in Kgalagadi District reach extremes, with maximum summer exceeding 40°C, and winter colds that can be as low as -5°C (Department of Meteorology *unpublished data*). There are three seasons; hot and wet (January to April), dry and cold (May to August), and hot and dry (September to December) (Knight, 1995; Van Rooyen & Van Rooyen, 1998). Soils of the Kalahari are mostly sandy with poor fertility, and are unable to hold surface water. The numerous pans scattered in the homogeneous sandveld are characterised by relatively higher mineral and saline clay soils with no vegetation, to hard grey soils which can support vegetation (Parris & Child 1968).

Vegetation is mainly open shrub savannah with tufted perennial grasses and grassed sand dunes towards the south (Botha & Mills, 1977; Skarpe, 1986; Knight, 1995). Vegetation changes along the rainfall gradient from the north, dominated by more water dependent species, to the south, converting to more open grass savannah with scattered shrubs of *Acacia spp.* and more species of karoo origin (Botha & Mills, 1977; Skarpe, 1986; Knight, 1995).

The arid Kalahari ecosystem supports many migratory ungulates, such as blue wildebeest, eland (*Taurotragus oryx*), red hartebeest (*Alcelaphus buselaphus*), kudu (*Tragelaphus strepsiceros*), gemsbok, springbok, steenbok (*Raphicerus camelus*), grey duiker (*Sylvicapra grimmia*) (Smithers, 1983; Skinner & Smithers, 1990). Predators in Kgalagadi include lion (*Panthera leo*), leopard (*Panthera pardus*), cheetah (*Acinonyx jubatus*), black backed jackal (*Canis mesomelas*), brown hyena (*Hyaena brunnea*), and spotted hyena (*Crocuta crocuta*) (Smithers, 1983; Skinner & Smithers, 1990). Predators are mostly distributed along Nossob valley (DWNP predator surveys *unpublished data*).

#### **Data Collection**

Ground survey population estimate data has been collect inside KTP since 1998 to 2008 missing only 2002. Data was collected from a slow moving vehicle by using the line transect

distance sampling method (Buckland *et al.* 2001). Existing tourist roads have been used since the beginning of the surveys. Though transects were not randomly placed and straight, as required for distance sampling (Buckland *et al.* 1993), the surveys were only used for comparative purposes rather than proper population estimates. The same transects had been surveyed each year on a monthly basis, but some transects were not survey as often as the others. Five transects which were regularly surveyed, were therefore selected and these were; Tworivers-Nossob (170 km), Nossob-Union's end (134 km), Polentswa-Khaa (136 km), Mabuasehube pans (142 km), and Khaa-Swart Pan (122 km).

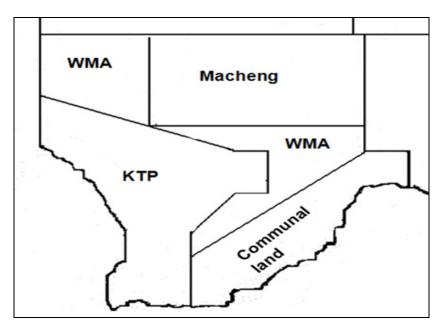
Dry season data (July–September) was used for population estimates by selecting one of the surveyed months giving first priority to July, August then September, respectively, depending on which month a survey was conducted in that year. Dry season months were selected in order to take advantage of increased visibility and reduced springbok movement because of very little or no rainfall which has been found to influence herd size and likely springbok migration (Bigalke, 1972; Botha & Mills, 1977; Stapelberg *et al.* 2008). These months were also selected so that ground survey population estimate trends can be compared with the KTP aerial survey trends. In Kgalagadi springbok lambing starts in early October and peaks in mid October. Lambing, however, continues throughout the wet season and into the beginning of the dry season as neonates, one week old, were observed from October up to June (*Pers. obs.*). Young animals (0-6 months old) and Juveniles (6-12 months old) where combined and termed lambs.

In addition to ground surveys, population trends for the entire Kgalagadi District, including KTP, was obtained from the Dry season (July-September) aerial survey population estimates. Aerial surveys were conducted for the years 1992, 1994, 1996, 1999, 2001, 2002, 2003, 2004, 2005, and 2007. Aerial survey data was collected using the stratified systematic transect sampling (Norton Griffiths, 1978) and density estimates for each species in each stratum, have been obtained using Jolly's (1969) method for sampling blocks of unequal size.

# Data Analysis Populations trends and distribution

Data analyses for population trends in KTP was done using DISTANCE 5.0 to estimates population for three species (springbok, gemsbok, and wildebeest) with which springbok has been found to be associated with (Skinner & Louw, 1996). Uniform and half-normal models in distance with cosine or simple polynomial expansions were used for the analysis and the model with the least Akaike's Information Criterion (AIC) was chosen as the best model (Buckland *et al.* 1993). Regression analysis was used to test significance of population trends of the three species in KTP and Kgalagadi District at  $P \le 0.05$ . In many of the transects, the required minimum observation of 60 (Buckland *et al.* 2001) was not achieved, therefore length of transects were summed up and total distance used in the estimates. This total distance changed in some years as some transects were not surveyed in those years. An area of 26,491 km<sup>2</sup>, adopted from the DWNP aerial surveys, was used as the total area of KTP. A

Survey areas in Kgalagadi district, from aerial surveys, have been divided into seven survey blocks. Communal land, which are dominated by pastoral farming, in southern Kgalagadi were surveyed separate while in the northern Kgalagadi one survey block combined communal land with WMAs. This block comprised about 50% communal land and 50% WMAs (Fig 1 & 2). This block, called Macheng, is therefore analysed separately for annual density changes, thus dividing the district into four land use areas, KTP, WMAs, Communal land areas, and Macheng (Fig 2). General Linear model was used to test the variation in ungulate density with area, and year, and results were tested for significance at  $P \le 0.05$ .



**Figure 2.** Map of the study area showing aerial survey blocks in Kgalagadi District, south-western Botswana.

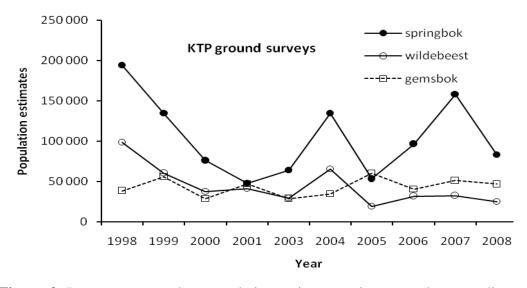
# Rainfall and populations

Climate data (rainfall) was tested for variation through regression analysis in the last 38 years at  $P \le 0.05$ . Rainfall data was also correlated with population trends through Pearson correlation analysis at  $P \le 0.05$ . Population estimates from both ground and aerial surveys were correlated with climatic data, and among the three ungulate populations. The effect of rainfall on the ration of lamb/female in springbok was examined by correlating previous rain season rainfall amounts with the consecutive year ration of lamb/female, to determine if the population responded to high or low rainfall years. Lamb counts from October to December were excluded from the estimates of the annual recruitment rate to avoid double counts. Thus lamb/female ratio was obtained by dividing a total number of all lambs recorded from January to September with the total number of females observed during the same period. Management activities and other activities within the study area were also assessed, through general information and personal experience of working in the study area, to determine other possible effects on the ungulate populations and distribution.

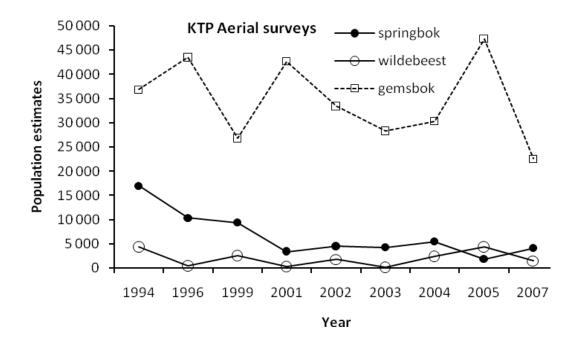
#### RESULTS

#### **Population trends and distribution**

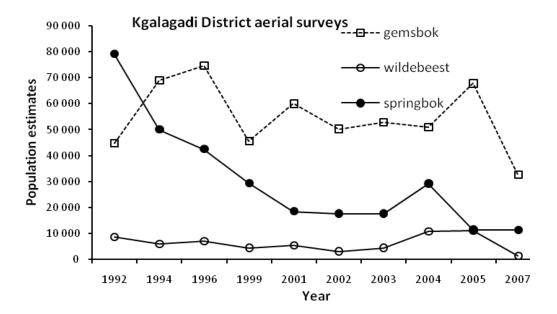
Ground survey ungulate population estimates gave much higher estimates than aerial surveys (Fig. 3 & 4). Even though these are not comparable they show similar population trends. KTP Ground survey from 1998 to 2001 show a significant population decrease ( $R^2$ =97.7%; P=0.01; DF=3) followed by no significant change in the population after 2001 ( $R^2$ =24.5%; P=0.26; DF=6) (Fig. 3). District Aerial surveys show a significant decrease of springbok population from the 1990s to 2007 ( $R^2$ =82.8%; P=0.000; DF=9). From aerial surveys, annual population estimates of gemsbok fluctuated throughout the years for KTP and the entire district (Fig. 4 & 5) and showed no significant change in the population in Kgalagadi neither from KTP ground surveys ( $R^2$ =4.9%; P=0.55; DF=9) nor from district aerial surveys ( $R^2$ =10.9%; P=0.34; DF=9). From KTP ground counts, wildebeest populations showed a significant decrease ( $R^2$ =47.3%; P=0.03; DF=9) and no significant change in population from aerial surveys ( $R^2$ =47.3%; P=0.03; DF=9) and no significant change in generation from the showed a significant change in the population showed a significant decrease ( $R^2$ =47.3%; P=0.03; DF=9) and no significant change in generation from the showed a significant decrease ( $R^2$ =47.3%; P=0.03; DF=9) and no significant change in population from aerial surveys ( $R^2$ =47.3%; P=0.03; DF=9) and no significant change in population from the populaticant ch



**Figure 3.** Dry season ungulate population estimates using ground counts distance sampling methode from in Kgalagadi Transfrontier Park, Botswana.



**Figure 4.** Dry season aerial wildlife population estimates using Jolly's (1969) method for sampling blocks of unequal size, in Kgalagadi Transfrontier Park, Botswana.



**Figure 5.** Dry season aerial wildlife population estimates using Jolly's (1969) method for sampling blocks of unequal size, in Kgalagadi District, Botswana.

Springbok densities varied significantly among areas (P=0.000; DF=34), and over the years (P=0.001; DF=34) in Kgalagaid. Communal areas had the highest springbok densities (Table

1). Gemsbok densities were significantly different among areas (P=0.000; DF=34) but there was no significant variation in density over the years. KTP had the highest gemsbok densities followed by WMAs, communal areas, and then Macheng (Table 1). For wildebeest, densities also varied among all the areas (P=0.03; DF=34) and had no significant variation over the years. Communal areas had the least wildebeest density while the other areas had similar densities (Table 1).

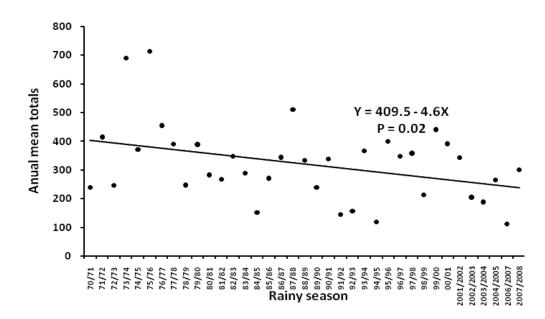
		KTP	Areas outside KTP			
Year	Species					
			WMAs	land	Macheng	
1994	Springbok	0.56	0.28	0.85	0.47	
	Gemsbok	1.21	0.88	0.20	0.26	
	Wildebeest	0.15	0.02	-	0.04	
1996	Springbok	0.34	0.51	0.54	0.30	
	Gemsbok	1.43	0.92	0.06	0.26	
	Wildebeest	0.18	0.09	-	0.17	
1999	Springbok	0.34	0.02	0.88	0.17	
	Gemsbok	0.98	0.55	0.23	0.05	
	Wildebeest	0.09	0.07	-	0.01	
2001	Springbok	0.09	0.06	0.39	0.29	
	Gemsbok	1.41	0.55 0.08		0.09	
	Wildebeest	0.01	0.10	-	0.11	
2002	Springbok	0.15	0.04	0.26	0.05	
	Gemsbok	1.10	0.46	0.26	0.05	
	Wildebeest	0.06	-	0.06	0.01	
2003	Springbok	0.14	0.07	0.54	0.09	
	Gemsbok	0.94	0.67	0.29	0.11	
	Wildebeest	0.01	0.10	-	0.07	
2004	Springbok	0.18	0.08	0.66	0.41	
	Gemsbok	1.00	0.57	0.16	0.14	
	Wildebeest	0.08	0.15	0.09	0.12	
2005	Springbok	0.06	0.12	0.32	0.08	
	Gemsbok	1.55	0.76	0.05	0.03	
	Wildebeest	0.14	0.20	-	0.07	
2007	Springbok	0.14	0.06	Not surveyed	0.22	
	Gemsbok	0.75	0.34	Not surveyed	0.06	
	Wildebeest	0.05	-	Not surveyed	0.002	
Mean	Springbok	0.22 (0.16)	0.14 (0.19)	0.55 (0.23)	0.23 (0.15)	
(±SE)	Gemsbok	1.15 (0.27)	0.63 (0.19)	0.17 (0.09)	0.12 (0.09)	
	Wildebeest	0.09 (0.06)	0.08 (0.07)	0.02 (0.04)	0.07 (0.06)	

 Table 1. Dry season population densities (No/ km<sup>2</sup>) of springbok, gemsbok, and wildebeest

 in four land use areas in Kgalagadi District, Botswana.

## **Rainfall and populations**

Average total rainfall in Kgalagadi showed a significant ( $R^2=13.9\%$ ; P=0.02; DF=36) decrease with an average of 322.41 (133.35 SD) mm (for Tsabong and Tshane) in that last 38 years. Total mean annual rainfall fluctuates a lot, with some years getting much below average rainfall and some years having much above average rainfall (Fig 6).



**Figure 6.** Mean annual rainfall totals (Tsabong and Tshane) in Kgalagadi district, Botswana. Data from Botswana meterological department.

There is no statistical significant correlation between springbok population and annual rainfall for neither KTP ground counts nor for Kgalagadi aerial surveys. The only ungulate that shows a statistically significant correlation to rainfall is the gemsbok from District aerial surveys ( $\rho$ =0.806; P=0.005) (Table 2). There is no statistical significant correlation between the springbok lamb/female ration and rainfall ( $\rho$ =-0.344; P= 0.33). Kgalagadi District aerial surveys shows a strong negative correlation between livestock and springbok ( $\rho$ =-0.835; P=0.005). Springbok population showed a significant positive correlation with wildebeest population ( $\rho$ =0.765; P=0.01) for KTP (Table 2).

**Table 2.** Correlation analysis of springbok population in relation to total annual rainfall, wildebeest, Gemsbok, and livestock population in Kgalagadi Transfrontier Park and Kgalagadi District. Botswana. ( $\rho$  =Pearson correlation coefficient)

		Rainfall		Springbok		Wildebeest		Gemsbok	
		КТР	Kgalagadi	КТР	Kgalagadi	КТР	Kgalagadi	Kgalagadi	
Springbok	ρ	0.337	-0.007						
	P-values	0.340	0.985						
Wildebeest	ρ	0.170	0.067	0.765	0.257				
	P-values	0.639	0.854	0.010	0.474				
Gemsbok	ρ	0.164	0.806	-0.004	0.111	-0.204	0.277		
	P-values	0.651	0.005	0.990	0.761	0.572	0.470		
Livestock	ρ		0.160		-0.835		-0.337	-0.201	
	P-values		0.682		0.005		0.375	0.604	

# DISCUSSION Population trends and distribution *Effect of rainfall*

Rainfall fluctuations in Kgalagadi showed no direct influence on population fluctuations of gemsbok and wildebeest in KTP, but seem to have an influence on the springbok population in KTP. Kgalagadi District received below average rainfall starting from 2002 (Fig. 6). This corresponds with greater fluctuations of springbok population estimates from ground counts in KTP during the same period (Fig. 3). Ground survey estimates in KTP show higher population estimates of springbok following poor rainfall seasons of 2003/2004 and 2006/2007 (Fig 3 & 6). Springbok is known to survive in areas without surface water (Smithers, 1983; Spinage & Matlhare, 1992), however, Nagy and Knight (1994) found that though springbok did not require regular intake of water it needs to have access to quality food resources, food with high water content, in order to be able to maintain body condition. In drought years water-supplement plants (tsama melons (*Citrullus lanatus*), wild cucumber

(Cucumis africanus), and gemsbok cucumber (Acanthosicyos naudinianus)), which most ungulates rely on in the Kalahari during the dry season are greatly reduced (Knight, 1995) thus springbok as well would be affected by rainfall. In 2007 poor rainfall was followed by large numbers of animals migrating into communal lands, and across Botswana-South Africa international border (Pers. obs.). The effect of the low rainfall was more pronounced for the more water dependent elands which were reported to have migrated southwards and crossed into neighbouring South Africa in large numbers. Aerial census of 2007 also reflect the effect of less rain in that year as less numbers of elands and wildebeest were recorded during the survey (DWNP aerial surveys, 2007). The fluctuation in springbok numbers in KTP from 2002 to 2008, could be indicative of the effect of poor rainfall over these years resulting in less suitable resources for the springbok in the rest of Kgalagadi thus making it more water dependent. More animals may be moving into KTP to access water from the artificial waterholes hence the greater fluctuations in the population in the dryer years. Ground surveys by DWNP also show that Springbok in KTP has high abundance, and is found all year around along the Nossob valley (DWNP unpublished data) likely due to the establishment of waterholes in this section of the park. Among the three species in KTP, wildebeest, distributed mostly along the Nossob valley (DWNP unpublished data), is the most water dependent (Knight & Knight-Eloff, 1988). Since the establishment of waterholes wildebeest in KTP has become less migratory (Knight & Knight-Eloff, 1988) therefore fluctuations in rainfall may have minimal influence on the population, as seen in my findings. Gemsbok seems to have a lesser reliance on surface water than wildebeest, as their distribution is relatively more widespread (DWNP unpublished data) hence will have less reaction to rainfall fluctuations.

#### Effect of forage suitability

Springbok occurred in high densities in communal land (Fig. 6) compared with other ungulates (Table 1). Verlinden *et al.* (1998) also found that springbok was relatively more common within livestock areas while gemsbok avoided these areas. Springbok have been found to prefer high quality forage rather than quantity (Skinner *et al.* 1987) therefore

preference of these areas, regardless of disturbance from human, is likely due to the preference of forage quality and short grasses, that is preferred by springbok, resulting from grazing by livestock (Skinner *et al.* 1987; Skinner & Smithers, 1990). Moderate grazing has been found to improve net primary productivity, nutrient content and ultimately foraging efficiency (McNaughton, 1976; Paige & Whitham, 1987; Moe & Wegge, 2008). In addition to forage quality, communal areas also have a high number of pans which springbok uses for mineral licks (*pers. obs.*) to supplement lack of minerals in their diet (Knight & Knight-Eloff, 1988).

Springbok are commonly associated with blue wildebeest and gemsbok (Skinner & Louw, 1996). Springbok grazes at a lower level and is a selective feeder, whereas wildebeest, a bulk feeder, grazes at a higher level than the springbok (Skinner & Louw, 1996; Knight, 1995; Stapelberg et al. 2008) suggesting a possible facilitation relationship between these species. Facilitation has been found to play a major role among some organism by improving conditions for organism existing together at individual or communities level (Bruno et al. 2003). McNaughton (1976) found that in Serengeti migratory wildebeest facilitated grazing for Thomson's gazelle, a selective feeder and morphologically similar to springbok, by removing the coarse layer of the grass hence Thomson's gazelle was found to prefer areas that were recently grazed by wildebeest. From the close association of springbok and wildebeest (Skinner & Louw 1996), it is likely that wildebeest population has an influence on the springbok population as there seem to be a forage quality facilitation created by wildebeest. Sharp decline in wildebeest population and other lager ungulates following the erection of fences and drought around Botswana in the 1980s (Williamson & Williamson, 1984; Spinage, 1992) would consequently result in a negative impact on the facilitation relationship that exist between springbok and bulk grazers, in particular the blue wildebeest. Grazing by livestock and lager ungulates, facilitate increase in nutritional value, and stimulate sprouting of new shoots which are more nutritional than the coarse grass (McNaughton, 1976; Paige & Whitham, 1987; Moe & Wegge 2008) hence springbok would find grazed areas more suitable in the dry season.

Communal areas, however, seem to have more negative factors for the springbok population compared with the rest of the study area. Kgalagadi has high incidents of illegal offtake, especially in communal areas and WMAs (*pers. obs.*). Illegal offtake has been found to have negative effects on wildlife populations (Newmark, 1996; Ngwamotsoko, 1997; Osborn & Parker, 2003), therefore springbok in communal areas may be subjected to such activities resulting in general population decline. Livestock numbers have increased in Kgalagadi (Campbell, 1997) and have displaced wildlife from the pans which are an important resource (mineral licks) for wildlife in Kalahari (Parris & Child, 1968). Despite the higher occurrence of springbok in communal areas, competition between wildlife and livestock cannot be excluded as a factor regulating wildlife population, including springbok, in Kgalagadi and may explain the negative correlation of the springbok population to livestock (Table 2).

Stapelberg *et al.* (2008) suggest that competition between wildebeest and springbok cannot be ruled out as a regulating factor of the springbok population in Kalahari, as suggested between the wildebeest and Thomson'e gazelle in Serengeti by Sinclair & Norton-Griffiths (1982). The negative impact of the wildebeest population on the springbok population in the Kgalagadi and KTP would be minimal as competition would be more pronounced only in the Nossob valley, where the interaction among these species is more pronounced as these species have become less migratory because of water provision (Knight & Knight-Eloff ,1988; DWNP *unpublished data*).

For the large ungulates human disturbance in terms of encroachment, and utilization is likely the deterrent factor in the communal areas as also suggested by Verlinden *et al.* (1998). Larger ungulates have been found to be more tolerant of poor forage quality enabling them to survive on a wider range of habitats compared to smaller ungulates (Bell, 1982; du Toit & Cumming, 1999). Gemsbok will therefore cope better with low forage quality in KTP and WMAs explaining their higher density, in these areas (Table 1). Safari hunting in WMAs take place from May to September which coincide with the aerial survey times therefore distribution of large game in WMAs could be highly influenced by the hunting exercise during this time of the year, thus displacing animals from these areas.

#### Effect of fire management practice

Management activities such as fire policies can exacerbate the decline in populations of ungulates if not administered properly, at the same time they can improve foraging efficiency for ungulates. Fire is one of the key ecological determinants of vegetation structure, floristic composition, and its distribution (Parr & Chown, 2003) and together with grazing, soils and climates they determine the function of savannah communities (Skarpe, 1992; Bond & Keeley, 2005). Studies have shown that burning increased overall nutritional quality of grass (Moe & Wegge, 1997) and ungulates were attracted to burnt areas more than nonburnt areas (Moe, Wegge & kapela, 1990; Moe & Wegge, 1997; Hassan *et al.* 2008). Management in KTP excludes fire from the park by means of fire breaks, thus the park rarely experience fire, while in WMAs and communal areas fire burns relatively frequently (*pers. obs*). Though fire has been viewed as detrimental to many systems (Mentis & Bailey, 1990; Bond & Archibald, 2003), resulting in the exclusion of fires from many ecosystems (Parr & Brokett, 1999), it has been used in many savannah systems and is known to improve forage quality for herbivores (Moe & Wegge, 1997; van Langevelde *et al.* 2003; Vermeire *et al.* 2004; Hassan *et al.* 2008).

The attraction of springbok to the communal areas could also be, in addition to livestock grazing and mineral licks, a result of frequent fires in these areas that is likely to result in better forage quality. The absences of fire in KTP, and the high frequency of fires in WMAs and communal lands is likely the key ecological factor that determines the distribution and abundance of ungulates between KTP and the surrounding WMAs.

# Effect of water provision

Infrastructure development, management activities, illegal offtake, and encroachment into wildlife areas have displaced and change migratory species behaviour (Parris & Child, 1968; Knight & Knight-Eloff, 1988; Williamson *et al.* 1988). These activities often result in loss of access to valuable habitats, isolated populations, and increased competition between livestock

and wildlife (Primack, 1996; Verlinden *et al.* 1998). Water provision has also been found to increase interspecific competition among wildlife species, increase depredation, and overutilization of available resources, and allow establishment of larger number of predators (Walker *et al.* 1987; Parker & Witkowski, 1999; Smit & Grant, 2009). Predators, especially the black backed jackal a versatile feeder, have a high occurrence along Nossob valley (DWNP *unpublished data*). Black backed jackal may have a negative effect on the survival of young springbok in this section of the park as this predator preys on young springbok (*pers obs.*). Wildebeest in KTP, especially along Nossob valley, have become less migratory because of water provision (Knight & Knight-Eloff 1988), springbok as well seem to spend most part of the year along Nossob valley (*pers. obs.*) thus forage resources may be overutilized by the higher numbers of these species resulting in competition among these species. Water provision for livestock in communal areas, can also attract springbok into these areas exposing them to competition for resources with livestock and persecution by humans.

#### **Rainfall and populations**

There is no significant correlation between rainfall and springbok population estimates for neither aerial surveys nor ground counts likely owing to the fact that springbok can survive well without free water (Smithers, 1983; Spinage & Matlhare, 1992; Nagy & Knight, 1994) thus rainfall may have minimal direct effect on springbok population. Though the current extent of migration of springbok in Kalahari region of Botswana is not well known, ungulates in the Kalahari are known to migrate between Central Kgalagadi Game Rreserve, in the north, and KTP (Williamson & Mbano, 1988; Williamson *et al.* 1988; Thouless, 1997). Springbok may therefore react by moving in or out of these areas depending on which area has better conditions, hence the correlation may not be pronounced. Because of the patchiness of rainfall in Kgalagadi recorded rainfall at the two stations, which are distant from KTP and WMAs, may not be representative of the entire study area. Areas in KTP and WMAs may receive better or worse rains thus providing better or poorer conditions for the

springbok. The negative correlation of rainfall to lamb/female ratio, may suggest that recruitment rate was not affected by rainfall fluctuations. Visibility may also have an effect on the number of young animals sighted as good rains would provide cover reducing visibility for young animals, on the other hand, poor rains would result in increased visibility and more animals would congregate at permanent water places, such as Nossob valley, therefore more young animals would be sighted, hence the negative correlation. There is no indication that springbok lamb/female ratio is directly affected by rainfall.

## CONCLUSION

Understanding different levels of ungulate interaction, population dynamics, and effects of human activity is a key role in management of viable wildlife populations. Current initiatives in conservation are aimed at establishing links between isolated habitats and areas of high biodiversity (MacDonald, 2003; Osborn & Parker, 2003). There is, however, a need for sound management of protected areas so that they remain suitable for a larger variety of species, therefore establishment of protected areas and migratory corridors alone is not enough in trying to curb the problem of population decline. KTP does not seem to offer favourable conditions for springbok as more animals are found outside the protected area.

Though there is limited knowledge on the effect fire on many faunal species (Davis *et al.* 2000; Trollope & Trollope, 2002; Collett, 2003; Parr & Chown, 2003; O'Reilly *et al.* 2006; Hassan *et al.* 2008) fire can still be used in KTP to create suitable habitats within the more secure areas, as it has proved beneficial to ungulates in some savannas (Moe, Wegge & kapela, 1990; van Langevelde *et al.* 2003; Vermeire *et al.* 2004; Hassan *et al.* 2008). "Patch mosaic burning" (PMB), a practice promoted for its ability to provide refuge areas for many species during fires (Brockett, Biggs & van Wilgen, 2001), with sound implementation and practise as recommended by Parr and Anderson (2006), could be practised in KTP and the surrounding areas to improve forage quality. Important resources such as pans outside KTP and WMAs have been lost for the springbok (Parris & Child 1968, Verlinden *et al.* 1998), however, areas in KTP and WMAs still offer such resources. Forage quality as a result of reduced grazing and fire is likely to make the park unfavourable for the springbok. Springbok

population decline in Kalahari may therefore be affected by management practices which fall short on making protected areas more suitable for wildlife. However there is need for more studies on the effect of different fire regimes on sward structure and grazing in the Kalahari, particularly Kgalagadi, before fire can be used effectively as a management tool for forage quality enhancement. There is also a need to do more research on the seasonal migrations of springbok, and interspecific competition along Nossob valley and the level of predation by jackals on springbok and its effect on survival rate of young animals.

## ACKNOWLEDGEMENTS.

I will like thank my supervisor Dr Stein R. Moe for the endless help and patience on the preparation of this thesis. I will also like to acknowledge Ellen Sandburg, Ronny Steen, Dr Ole-Gunner Støen for thei assistance with statistics and data analysis. I am also grateful to my class mates /friends Yun Fang, Martin Skram Vatne, Linn-Susan Rotås, and Linda Marie Stakkeland, Laura Sofia Luna Maira, with whom discussions brought more light into the writing of my thesis. I will also like to thank my colleagues at work who provided me with all the information I needed and field assistance for my studies.

#### REFERENCES

- ARNTZEN, J. W. & VEENENDAAL E. M. (1986) A Profile of the Environment and Development in Botswana. Amsterdam: Free University. 172 pp.
- BELL, R.H.V. (1982) The effect of soil nutrient availability on community structure in African ecosystems. In: Huntley, B.J. & Walker, B.H. (eds.) *The ecology of tropical savannas. Ecological Studies* 42, pp. 193-216. Springer Verlag, Berlin, DE.
- BERGSTRÖM, R., & SKARPE, C. (1999) The abundance of large wild herbivores in a semi-arid savanna in relation to seasons, pans and livestock. *Afr. J. Ecol.* **37**, 12-26.
- BIGALKE, R.C. (1972) Observations on the behaviour and feeding habits of springbok, Antidorcas marsupialis. Zool. Afric. 7, 333-359.
- BOND, W. J. & KEELEY J. E. (2005) Fire as a global 'herbivore': the ecology and evolution of flammable ecosystems. *Trends Ecol. Evol.* **20**, 387-394.
- BOND, W.J. & ARCHIBALD, S. (2003) Confronting complexity: Fire policy choices in South African savanna parks. *Int. J. Wildland Fire* 12, 381-89.
- BONIFICA. (1992b) Technical Assistance to the Central Kalahari Borehole Project. Gaborone, Botswana: Department of Wildlife and National Parks. 234 pp.
- BOTHMA, J. du P. & MILLS, M.G.L. (1977) Ungulate abundance in the Nossob River Valley, Kalahari Desert. *Proceedings of the XIII<sup>th</sup> International Congress of Game Biologists, Atlanta, Georgia*, pp. 90-102.
- BROCKETT, B. H., BIGGS, H. C. & VAN WILGEN B.W. (2001) A patch mosaic burning system for conservation areas in southern African savannas. *Int. J. Wildland Fire* 10, 169-183.
- BRUNO, J. F., STACHOWICZ J.J. & BERTNESS, M. D. (2003) Inclusion of facilitation into ecological theory. *Trends Ecol. Evol.* **18**, 119-125.
- BUCKLAND, S. T., ANDERSON, D. R., BURNHAM, K. P., LAAKE, J. L., BORCHERS,D. L. & THOMAS, L. (2001) *Introduction to distant sampling: estimating abundance* of biological populations. Oxford University Press, Oxford. 432 pp.

- BUCKLAND, S.T., ANDERSON, D.R., BURNHAM, K.P. & LAAKE, J.L. (1993) Distance Sampling: Estimating Abundance of Biological Populations, Chapman & Hall, London, reprinted (1999) by Research Unit for Wildlife Population Assessment, St Andrews.
- CAMPBELL, A. (1997) A history of wildlife in Botswana to 1966. In Proceedings of a national conference on conservation and management of wildlife in Botswana.Department of Wildlife and National Parks and Kalahari Conservation Society. pp 7-31.
- CHILD, G. & Le RICHE, J.D. (1969) Recent springbok treks (mass movements) in south-western Botswana. *Mammalia* **33**, 499-504.
- COLLETT, N. (2003) Short and long-term effects of prescribed fires in autumn and spring on surface-active arthropods in dry sclerophyll eucalypt forests of Victoria. *Forest Ecol. M*gmt. **182**, 117-138.
- COOKE H.J. (1985) The Kalahari Today: A Case of Conflict Over Resource Use. *Geog. J.* 151,75-85.
- DAVIS, M. A., PETERSON, D. W., REICH, P. B., CROZIER, M., QUERY, T., MITCHELL, E., HUNTINGTON, J. & BAZAKAS, P. (2000) Restoring savanna using fire: impact on the breeding bird community. *Restor. Ecol.* 8, 30-40.
- DEPARTMENT OF METEOROLOGY, Ministry of Environment Wildlife and Tourism, Gaborone.
- DWNP (Department of Wildlife and National Parks) Dry Season Aerial Census of Animals in Botswana reports. Monitoring Unit Research Division, Ministry of Environment Wildlife and Tourism, Gaborone.
- DU TOIT, J.T. & CUMMING, D.H.M. (1999) Functional significance of ungulate diversity in African savannas and the ecological implications of the spread of pastoralism. *Biod. Conservat.* 8, 1643-1661.
- HASSAN, S. N., RUSCH, G. M., HYTTEBORN, H. SKARPE, C. & KIKULA, K. 2008. Effects of fire on sward structure and grazing in western Serengeti, Tanzania. Afr. J. Ecol. 46, 174-185.

- JOLLY, G.M. (1969) Sampling methods for aerial censuses of wildlife populations. *East Afr. Agr. Forest. J.* **34**, 46 49.
- KGALAGADI DDP 6. (2007) Kgalagadi District Development Plan number 6, Tsabong.
- KNIGHT, M.H. & KNIGHT-ELOFF, A.K. (1988) The importance of borehole water and lick sites for Kalahari South Africa ungulates. *J. Arid Environ.* **15**, 269-282.
- KNIGHT, M.H. (1995) Tsamma melons, *Citrullus lanatus*, a supplementary water supply for wildlife in the southern Kalahari. *Afr. J. Ecol.* **33**, 71-80.
- MACDONALD, M. A. (2003) The role of corridors in biodiversity conservation in production forest landscapes: A literature review. *Tasforests* **14**, 41-52.
- MCNAUGHTON, S. J. (1976) Serengeti migratory wildebeest: Facilitation of energy flow by grazing. *Science* **191**, 92-94.
- MENTIS, M.T. & BAILEY, A.W. (1990) Changing perceptions of fire management in savanna parks. J. Grassl. Soc. South. Af. 7, 81-85.
- MOE, S.R., WEGGE, P. & KAPELA, E.B. (1990) The influence of man-made fires on large wild herbivores in Lake Burungi Area in Northern Tanzania. *Afr. J. Ecol.* **28**, 35-43.
- MOE, S. R. & WEGGE, P. (1997) The effects of cutting and burning on grass quality and axis deer (Axis axis) use of grassland in lowland Nepal. *J. Trop. Ecol.* **13**, 279-292.
- MOE, S. R. & WEGGE, P. (2008) Effects of deposition of deer dung on nutrient redistribution and on soil and plant nutrients on intensively grazed grasslands in lowland Nepal. *Ecol. Res.* 23, 227-234.
- MORDI, A.R. (1989) The future of animal wildlife and its habitat in Botswana. *Environ. Conservat.* **16**, 147-156.
- NAGY, K. A., & KNIGHT, M. H. (1994) Energy, water, and food use by springbok antelope (*Antidorcas marsupialis*) in the Kalahari Desert. *J. Mammal.* **75**, 860-872.
- NEWMARK, W. D. (1996) Insularisation of Tanzanian parks and the local extinction of large mammals. *Conservat. Biol.* **10**, 1549-1556.
- NGWAMOTSOKO, K. T. (1997) Analysis of national policies affecting wildlife conservation in Botswana. In Proceedings of a national conference on conservation and management

of wildlife in Botswana. Department of Wildlife and National Parks and Kalahari Conservation Society. pp 176-185.

- NORTON-GRIFFITHS, M. (1978) Counting animals, 2nd ed. Handbook 1. African Wildlife Leader- ship Foundation, Nairobi, Kenya. 139pp.
- O'REILLY, L., OGADA, D., PALMER, T. M. & KEESING, F. (2006) Effects of fire on bird diversity and abundance in an East African savanna. *Afr. J. Ecol.* **44**, 165-170.
- OSBORN, F. V., & G. E. PARKER. (2003) Linking two elephant refuges with a corridor in the communal lands of Zimbabwe. *Afr. J. Ecol.* **41**, 68-74.
- OWEN-SMITH, R.N. (1988) Megaherbivores. The influence of very large body size on ecology. Cambridge University Press, Cambridge.
- PAIGE, K. N. & WHITHAM, T. G. (1987) Overcompesation in response to mammalian herbivory: the advantage to being eaten, *Am. Nat.* **129**, 407-416.
- PARKER, A.H. & WITKOWSKI, E.T.F. (1999) Long-term impacts of abundant perennial water provision for game on herbaceous vegetation in a semi-arid African savanna woodland. J. Arid Environ. 41, 309-321.
- PARR, C. L. & BROCKETT, B. H. (1999) Patch-mosaic burning: a new paradigm for savanna fire management in protected areas? *Koedoe*. **42**, 117-130.
- PARR, C.L. & ANDERSEN, A.N. (2006) Patch mosaic burning for biodiversity conservation: A critique of the pyrodiversity paradigm. *Conservat. Biol.* 20, 1610 -1619.
- PARR, C.L. & CHOWN, S.L. (2003) Burning issues in conservation: a critique of faunal fire research in Southern Africa. *Aust. Ecol.* 28, 384-395.
- PARRIS, R. & CHILD G. (1968) The importance of pans to wildlife in the Kalahari and the effects of human settlement on these areas. J. S. Wildl. Mgmt. Ass. 3, 1-8.
- PARRIS, R. & CHILD, G. (1973) The importance of pans to wildlife in the Kalahari and the effect of human settlement on these areas. *J. S. Wildl. Mgmt. Ass.* **3**, 1-8.
- PRIMACK, R. B. (2006) *Essentials of conservation biology* (4<sup>th</sup> ed). Sinauer Associates. Sunderland, Ma.

- RABOROKGWE, M. V. (1997) Cordon fences and wildlife issues. In Proceedings of a national conference on conservation and management of wildlife in Botswana. Department of Wildlife and National Parks and Kalahari Conservation Society. pp 114-120.
- SINCLAIR, A.R.E. & NORTON-GRIFFITHS, M. (1982) Does competition or facilitation regulate migrant ungulate populations in the Serengeti? A test of hypotheses. *Oceologia* 53, 364-369.
- SISK, T.D., LANNER, A.E., SWITKY, K.R. & EHRHICH, P. R. (1994) Identifying extinction threats. *Biosciences* 44, 592-604.
- SKARPE, C. (1986) Plant community structure in relation to grazing and environmental changes along a north–south transect in the western Kalahari. *Vegetatio* **68**, 3-18.
- SKARPE, C. (1992) Dynamics of savanna ecosystems. J. Veg. Sci. 3, 293-300.
- SKINNER, J. D. & LOUW, G. N. (1996) (EDS.) The springbok Antidorcas marsupialis (Zimmerman 1780). Transvaal Mus. Monogr. 10, 1-50.
- SKINNER, J. D. & SMITHERS, R. H. N. (1990) The mammals of the southern African subregion. University of Pretoria Press, South Africa.
- SKINNER, J. D. (1993) Springbok (Antidorcars marsupialis) treks. Trans. Roy. Soc. S. Af. 48, 291-305.
- SKINNER, J.D. & MOSS, D.G. (2004) Kgalagadi springbok (*Antidorcas marsupialis*): bucking the trend. *Trans. Roy. Soc. S. Af.* **59**, 119-121.
- SKINNER, J. D., DOTT, H. M., VAN AARDE, R. J., DAVIES, R. A. G. & CONROY, A.M. (1987). Observations on a population of springbok *Antidorcas marsupialis* prior to and during a severe drought. *Trans. Roy. Soc. S. Af.* 46, 191-197.
- SMIT, I. P. J., & GRANT, C.C. (2009) Managing surface-water in a large semi-arid savanna park: Effects on grazer distribution patterns. *J. Nat. Conservat.* On line early edition.
- SMITHERS, R. H. N. (1983) The mammals of the southern African subregion. University of Pretoria Press, South Africa.

SPINAGE, C. A. & MATLHARE, J. M. (1992) Is the Kalahari cornucopia fact or fiction? A predictive model. *J. Appl. Ecol.* **29**, 605-610.

SPINAGE, C. A. (1992) The decline of the Kalahari wildebeest. Oryx 26, 147-150.

- STAPELBERG, H., VAN ROOYEN, M. W., BOTHMA, J. P., VAN DER LINDE, M. J. & GROENEVELD, H. T. (2008) Springbok behaviour as affected by environmental conditions in the Kalahari. *Koedoe* 50, 145-153.
- TAOLO, G. (1997) *The current status of wildlife in Botswana*: Proceedings of national conference on conservation and management of wildlife in Botswana. Pp 32-43.
- THOULESS C. R. (1997) Large mammals inside and outside protected areas in the Kalahari: In Proceedings of national conference on conservation and management of wildlife in Botswana. pp 59-74.
- TROLLOPE, W. S. W. & TROLLOPE, L. A. (2002) Fire behaviour a key factor in the fire ecology of African grasslands and savannas. In Forest Fire Research & Wildland Fire Safety, Viegas (ed.) Millpress, Rotterdam, ISBN 90-77017-72-0.
- VAN LANGEVELDE, F., DE VIJVER, C., KUMAR, L., DE KOPPEL, J., DE RIDDER, N.,
  VAN ANDEL, J., SKIDMORE, A.K., HEARNE, J.W., STROOSNIJDER, L.,
  BOND, W.J., PRINS, H.H.T. & RIETKERK, M. (2003) Effects of fire and herbivory on the stability of savanna ecosystems. *Ecology* 84, 337-350.
- VAN ROOYEN, N. & VAN ROOYEN, M.W. (1998) Vegetation of the south-western arid Kalahari: an overview. *Trans. Roy. Soc. S. Af.* **53**, 113-140.
- VERLINDEN, A. (1997) Land requirements for wildlife conservation in Botswana. In Proceedings of a national conference on conservation and management of wildlife in Botswana. Department of Wildlife and National Parks and Kalahari Conservation Society. Pp 112-113.
- VERLINDEN, A., PERKINS, J. S., MURRAY, M. & MASUNGA G. (1998) How are people affecting the distribution of less migratory wildlife in the southern Kalahari of Botswana? A spatial analysis. J. Arid. Environ. 38, 129-141

- VERMEIRE, L. T., MITCHELL, R. B., FUHLENDORF, S.D. & GILLEN, R. L. (2004) Patch burning effects on grazing distribution. *J. Range Manage*. **57**, 248-252.
- WALKER, B.H., EMSLIE, R.H., OWEN-SMITH, N.,& SCHOLES, R. J.(1987) To cull or not to cull: Lessons from a southern African drought. J. Appl. Ecol. 24, 381-401.
- WILLIAMSON, D. T. & MBANO, B. (1988) Wildebeest mortality during 1983 at Lake Xau, Botswana. Afr. J. Ecol. 26, 341-344.
- WILLIAMSON, D. & WILLIAMSON, J. (1984) Botswana's fences and the depletion of the Kalahari wildlife. *Oryx* 18, 218-222.
- WILLIAMSON, D., WILLIAMSON, J., & NGWAMOTSOKO, K. T. (1988) Wildebeest migration in the Kalahari. *Afr. J. Ecol.* **26**, 269-280.