The ecology of ungulates in the Waterberg Plateau National Park, Namibia

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DEDICATION

This thesis is dedicated to my father Mr. Kaembo Kasiringua, my wife Mbaungura Kasiringua and my two children, Avril Ngarijande Kasiringua and Otjari Kasiringua. Dad, words will never be enough to highlight the role that you have played in my life and the man that you have moulded me into. You told me to strive for what I believe in and that the only way to achieve ones goals was to firstly and most importantly set the goals. Your motivation and wisdom has surely paved a path for a once lost boy from the dusty streets of Tsumeb into a man that you will always be proud of.

PREFACE

The research contained in this thesis was completed by the candidate while based in the Discipline of Geography and Environmental Sciences, School of Environmental Sciences of the College of Agriculture, Engineering and Science, University of KwaZulu-Natal, Westville Campus, South Africa.

The contents of this work have not been submitted in any form to another university and, except where the work of others is acknowledged in the text, the results reported are due to investigations by the candidate.

Signed: Prof. Şerban Procheş

Date: 2 April 2019

DECLARATION 1: PLAGIARISM

I, Evert A. Kasiringua, declare that:

(i) the research reported in this dissertation, except where otherwise indicated or acknowledged, is my original work;

(ii) this dissertation has not been submitted in full or in part for any degree or examination to any other university;

(iii) this dissertation does not contain other persons' data, pictures, graphs or other information, unless specifically acknowledged as being sourced from other persons;

(iv) this dissertation does not contain other persons' writing, unless specifically acknowledged as being sourced from other researchers. Where other written sources have been quoted, then:

a) their words have been re-written but the general information attributed to them has been referenced;

b) where their exact words have been used, their writing has been placed inside quotation marks, and referenced;

(v) where I have used material for which publications followed, I have indicated in detail my role in the work;

(vi) this dissertation is primarily a collection of material, published as journal articles or presented as a poster and oral presentations at conferences. In some cases, additional material has been included;

(vii) this dissertation does not contain text, graphics or tables copied and pasted from the Internet, unless specifically acknowledged, and the source being detailed in the dissertation and in the References sections.

Signed: Evert A. Kasiringua

Date: 05 March 2019

DECLARATION 2: PUBLICATIONS

My role in each paper is indicated. The * indicates corresponding author.

1. **Kasiringua E., Kopij G*., Procheș Ș. 2017**. Daily activity patterns of ungulates at water holes during the dry season in the Waterberg National Park, Namibia // Russian Journal of Theriology. Vol.16. No.2. P.129–138. (*Published*)
2. **Kasiringua E*., Procheș Ș., Kopij G., Hove K. 2017.** Distribution, habitat use and abundance of ungulates in Waterberg National Park, Namibia. (*Submitted*)
3. **Kasiringua E*., Procheș Ș., Kopij G. 2018.** Population Structure of ungulates in Waterberg National Park, Namibia. (*Accepted for publication*)
4. **Kasiringua E*., Procheș Ș., Kopij G 2018.** Rainfall as the key indirect driver of African ungulates population dynamic (a Namibian case study). (*Ready for submission*)

The first study is a focuses on the daily activity patterns of ungulates at water holes during the dry season in the Waterberg National Park, Namibia. It was conceived and designed by the first author and the supervisors, Professor Şerban Procheş and Professor Gregory Kopij. The first author conducted the literature search while Professor Şerban Procheş and Professor Gregory Kopij validated the search outcomes.

The last three studies were conceptualized by the first author and both Professor Şerban Procheş and Professor Gregory Kopij. The first author proposed the design of the studies, collected as well as analysed the data, while the supervisors, Professor Şerban Procheş and Professor Gregory Kopij guided in the considerations for data collection and analysis. Prof Gregory Kopij guided in the statistical analysis of all the papers.

Signed: Evert A. Kasiringua

Date: 05 March 2019

GENERAL ABSTRACT

Although ungulate species form an important component of Namibia's economy through tourism, their population sizes vary substantially in relation to irregular rainfall, poaching, predation and competition, amongst other reasons. Understanding the ecology of ungulates is the key to adaptive ecosystem management and wildlife conservation in semi-arid savanna ecosystems. The study was conducted at Waterberg National Park, to determine habitat preferences, seasonal variation in population structure, daily drinking activities of twelve ungulate species and population dynamics of ungulates over a period of 33 years (1980-2013). The data used included road counts in all four vegetation types in the park (*Terminalia sericea-Melhania acuminata* vegetation, *Terminalia sericea-Thesium megalocarpum*, *Terminalia sericea-Blepharis integrifolia*, and the rock-inhabiting *Peltophorum africanum* community), waterhole counts, and pre-existing aerial counts. The probability of occurrence of large and medium ungulates was influenced by distance from the waterholes and from the roads. The population structure of seven herbivores varied in intricate ways between species and seasons. Smaller herds of ungulates were recorded most during the dry season as compared to larger herds observed during the wet season. Overall, the most frequent drinking times were between 15:00-22:00 with 18:00-19:00 being the conspicuous peak of the drinking activity, with 15% of animals in attendance. Four groups of ungulates were identified as per their drinking activity patterns: 1) day drinkers (warthog, giraffe, roan, and sable), 2) day/night drinkers (dik-dik, steenbok and common duiker), 3) evening/night drinkers (white rhino, black rhino and buffalo) and 4) night/morning drinkers (eland, gemsbok and kudu). The buffalo and eland population densities comprised together more than half of all ungulates recorded. Roan and sable antelope, kudu and warthog were also fairly common (with 5-12% of all ungulates recorded). White rhino, black rhino, giraffe, and gemsbok were classified as uncommon (together 11.9%), whilst the remaining seven species were rare (together 1.9%). Population size in eland showed a weak positive relationship with the annual average rainfall between the years 1981 - 2013, whereas population sizes in kudu, sable, gemsbok and roan showed a weak negative relationship with the amount of rain. No relationship was detected in giraffe, buffalo and hartebeest populations. The efficient management of wildlife resources that are economically and socially important necessitates regular surveys to monitor population trends in order to develop applicable management options.

Thus, monitoring methods which are practical and efficient and provide accurate data are required for sound wildlife management. The results generated from this study provide novel contributions to strengthening management and conservation efforts of ungulates in Waterberg National Park and other wildlife parks in Namibia. More studies in the area of diet analysis of grazers and browsers as well as their preferences for particular plant species, with emphasis on inter- and intra- species competition is recommended.

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First and foremost I would like to thank The Almighty God for granting me the strength and courage, spiritually and mentally throughout this entire study. It is impossible to embark on a study of this nature without the assistance of countless people. Great gratitude and heartfelt appreciation goes to both of my supervisors, Professor Şerban Procheş and Professor Gregory Kopij, firstly for accepting me as their student and for sharing their vast intellectual knowledge with me during this study. Their support during the data analysis and write-up was instrumental for the success of this study since without their intellectuality and academic professionalism this thesis would not have been written. I would like to thank the University of Namibia for granting me the opportunity to further my studies and also the School of Environmental Science, College of Agriculture, Engineering and Science, University of KwaZulu-Natal for accepting me as their student. In addition, I would like to thank the Namibia Student Financial Assistance Fund (N.S.F.A.F) for funding the project. I wish to acknowledge the Ministry of Environment and Tourism for providing me with the permits for data collection in W.N.P especially so the directorate of scientific services. Many thanks also goes to the W.N.P staff for their support and engagement during the two years of fieldwork, especially to Mr. David Masen, Mr. Mannie Le Roux, Mr. Bethold Kandjii, Mr. Thomas Kapia, Mr. Johannes Ndiili, and Mrs. Patience Kahundu. To my dearest parents, Mr. Kaembo Kasiringua and Mrs. Veueza Kasiringua and siblings, Ngaruuhe Kasiringua, Cosmos Shaduka, Tjivii Kandjii, Uaruuka Kasiringua and Collin Kandjii, my heart-felt gratitude goes to you for the unconditional love, words of encouragements, emotional support and being my pillar and strength through the course of this study. I am also grateful to my friends and research colleagues, Mr. Osadolor O. Ebhuoma, Ms. Ashyn L. Padayachee, Mr. Tony Nsio, Mr. Bryan Kariko, Dr. Jack Kambatuku, Mr. Siyamana Mulele, Mr. Frank Kahorongo, Mr. Dave Joubert, Professor Christina Skarpe, Mr. Cecil Togarepi, Mr Kudakwashe Hove, Mr. Oscar Mbango, Mr Barthlomew Chataika and I humbly thank you all for your individual contributions to my research and for the support especially during moments that I felt the weight of the world on my shoulders, your support and encouragements were instrumental in the course of this journey. To my wife, Mbaungura Pena Kasiringua I would like to firstly thank you for your contributions to my studies, but most importantly for your unconditional love and faith in me.

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CHAPTER 1: GENERAL INTRODUCTION

1.1 Ungulate populations in Africa and Namibia

Populations of wildlife species in Africa are declining (Gordon *et al*., 2004; Wilkie *et al*., 2011; Norton-Griffiths, 2000, 2007; Newmark, 1996, 2008; Otichillo *et al*., 2000; Ogutu & Owen-Smith, 2003; Caro & Scholte, 2007; Ogutu *et al*., 2009, 2011; Western *et al*., 2009; Scholte, 2011). This statement applies even to those populations found in protected areas, and this is due to disease outbreaks, irregular rainfalls, climatic fluctuations, poaching and other human activities within the wildlife habitats (Brashares *et al*., 2001; Milner-Gulland *et al*., 2003; Newmark, 2008; Tsindi *et al*., 2016; Chase *et al*., 2016). Du Toit (1995) pointed out that the rich wildlife resources of southern Africa hold considerable economic potential, but the options for maximizing and sustaining this potential are constrained by the ecological and human determinants of the wildlife communities in each particular ecosystem.

The population ecology of ungulates provides an understanding of how and why populations of animals fluctuate in size over a period of time. An understanding of this is vital for several disciplines, e.g. the conservation of these ungulates and their evolutionary biology (Gaillard *et al*., 1998; Mysterud *et al*., 2002). There are a number of environmental factors that influence population dynamics, and understanding these factors and their influences on populations is vital in the management and conservation of these species (Owen-Smith *et al*. 2005). Numerous ecological studies have shown that variations in abundance of ungulates, activity or the use of sites by ungulates is linked to the seasons, the scale of human activity, other species, or the availability of resources (Keuroghlian *et al*., 2004; Di Bitetti *et al*., 2008; Pérez-Cortez *et al*., 2012; Reyna-Hurtado *et al*., 2012; Pérez-Irineo *et al*., 2016).

Wildlife has long been a primary focus for wildlife managers and researchers in Namibia. Namibia has ungulate communities of unique diversity, and understanding the patterns of variation in abundance and structure of communities and the consequences for species diversity has been a focal point in ecology for many decades (see Hutchinson, 1959). Abiotic and biotic factors both contribute to the patterns of habitat utilization by herbivores in Africa (Jarman & Sinclair, 1979; Jenkins *et al*., 2002; Omphile & Powell, 2002). This is the case particularly within semi-arid environments, which vary in quality both spatially and temporally, perhaps more drastically than humid and mesic ones (Caughley, 1987; Buono *et al*., 2010). Namibia is one of the driest countries in southern Africa, with much of its land characterised by a semi-arid climate, with low and highly variable rainfall (Bann & Wood, 2012). The distribution of wildlife in Namibia is especially influenced by the irregular availability of rainfall, which in turn affects the quality and quantity of available forage for the wildlife, and hence the age and sex structures of the animal populations (Tsindi *et al*., 2016).

Equilibrium grazing/browsing systems are said to be characterized by climatic stability that results in predictable primary production (Behnke, 2000), whereas non-equilibrium grazing/browsing systems receive low and irregular rainfall that produces erratic fluctuations in forage supplies. In semi-arid countries like Namibia, these two types of environment present conservationists with very different management problems. Identifying and keeping the best stocking rates is beneficial in an equilibrium system since animals reproduce at a rate determined by the availability of primary production (Behnke, 2000). Unpredictable rainfall makes it difficult in non-equilibrium systems. Stocking rates have little value if fluctuation in rainfall has a stronger effect than animal numbers on the abundance of forage. In such an environment the ability to adjust stocking rates rapidly to track unexpected changes in feed availability is more beneficial. In semi-arid countries, specifically in Namibia the distinction between equilibrium and non-equilibrium systems centers on the reliability of rainfall (Behnke, 2000).

The seasonal and daily migration of wildlife are known to be controlled to a great extent by the availability of water (Wolanski & Gereta, 2001), and this is also true for their distribution within conservation areas (Sungirai & Ngwenya, 2016). The distribution of animals is therefore controlled by the availability of surface water, which mainly depends on rainfall except in cases where artificial water points are constructed and water supplied from boreholes (Hayward & Hayward, 2012). Recently, artificial water points have become the main source of water for wildlife in dry countries such as Namibia (Epaphras *et al*., 2007), which no doubt creates novel patterns in the distribution and population ecology of ungulates.

There are two main types of ecological controls on a population (Gandiwa, 2013; Fronhofer *et al*., 2017). Firstly, the bottom-up ecological control, which is the limitation placed by resources allowing growth such as food source, habitat, or space, and secondly the top-down ecological control, which is the limitation placed by factors controlling death such as predation, disease, or natural disasters (Gandiwa, 2013). Both the top-down and bottom-up ecological processes influence the size of ungulate populations (Grange, 2006; Sinclair, 2003). They may vary between different ecosystems, and their relative importance can vary spatially and temporally, with possible sudden shifts in top-down and bottom-up control occurring over time (Meserve *et al*., 2006; Sinclair, 2003; Gandiwa, 2013). These sudden shifts in top-down and bottom-up control are likely to occur in semi-arid ecosystems (Namibia) with inconsistent rainfall patterns (Holmgren *et al*., 2006; Gandiwa, 2013). This is evident in prevailing dry years, where resource-limited conditions lead to strong bottom-up control because of reduced plant productivity. During wet years, biotic interactions become more important as the abundance of consumers increase, and top-down control prevails (Meserve *et al*., 2006; Gandiwa, 2013).

Reliable monitoring and assessing of different ungulate species and their populations is a challenging process in the ecology of wildlife (Williams *et al*., 2001; Burton *et al*., 2015), more so for rare species that can be elusive and have a low probability of detection (Petit & Valiere, 2006; Guschanski *et al*., 2009). Several survey methods are used to estimate, monitor and manage ungulate populations. The choice of the best method depends on estimation accuracy, management objective and financial limitations (Rönnergård *et al*., 2007). Nonetheless, species population estimations are vital for population conservation and management to introduce certain preservation and regulation approaches (Eggert *et al*., 2003; Noon *et al*., 2012). This enables management and decision-making by providing reliable data on the number of animals, distribution, habitat use, individual growth rate, reproduction, sex/age composition, genetic variation and intraspecific interactions (Williams *et al*., 2001; Eggert *et al*., 2003).

Different field and laboratory methods can be used to estimate species densities and determine population sizes of ungulates in a given area. Several different survey methods have been used to monitor ungulate populations around the world, including aerial surveys, water hole counts, pellet group counts, direct observations and road counts. Three of these methods are commonly used in Southern African for ungulate management, i.e. aerial surveys, water hole counts and road counts. These methods however vary in terms of reliability, costs, information obtained and time period surveyed (Barnes, 2001, Campbell *et al*., 2004, Smart *et al*., 2004), which makes it difficult to select the most suitable method for management. Surveying approaches can be achieved directly or indirectly. Direct observations count the amount of detected animals via aerial, drive, waterhole or foot counts, whereas indirect counts are based on animal dung, tracks or feeding signs (Cromsigt *et al*., 2009). Indirect methods of ungulate estimates are difficult to achieve in most of Namibia's National Parks because of the dangers involved and the strict laws that prohibits one to walk on foot in the parks.

Nevertheless, for ungulates and particularly species that are difficult to detect using direct methods (e.g. aerial surveying), indirect methods like dung pellet group counts are widely used. Plhal *et al*. (2014) noted that counts of dung pellet groups are the most common and most accurate methods for determining animal numbers, even though they do not provide information on the sex ratio, age structure, activity patterns and population structure. Contrary to indirect methods of ungulate estimation, the direct surveying method (aerial counts, waterhole counts and foot counts) provides not only information about species abundance but also about habitat associations, activity patterns, behaviour, and community structure such as sex-ratio and age-structure (Rovero *et al.*, 2013; Flemming *et al.*, 2014). In WNP direct methods such as aerial surveys, 48hours waterhole counts and road counts have been the most accepted and frequently used method for monitoring population densities and trends.

Aerial counts are an important tool for wildlife management in Africa because of the vastness and remoteness of its many wildlife areas (Jachmann, 2002). Like many other sampling methods, aerial sampling has many sources of bias (visibily, density of the vegetation, size of the animal, cluster size and colouring of the animal), most of which can be avoided with a proper design (Jachmann, 2002). Generally, spotting and counting problems represent the most important source of bias in aerial techniques (Jachmann, 2002). According to Jachmann (2002), several techniques have been proposed to eliminate bias from aerial counts application and that the only practically feasible and theoretically sound technique is the double-count technique.

In road counts, typically a team of three observers follows a straight line of known length (Buckland *et al*., 1993; Jachmann 2002, Kiffner *et al.,* 2017). Each observation of animals is recorded, as well as the distance of the animals from the observer and the sighting angle. The sighting distances and sighting angles are then converted to perpendicular distances. A frequency diagram of grouped perpendicular distances will show the probability of detecting a group of animals of a particular species in a particular habitat at particular distances from the transect line. This detection function can be modelled with four different estimators depending on the shape (hazard, negative exponential, half normal and uniform) and three different adjustment terms (cosine, polynomial and hermite), using the program DISTANCE (Laake *et al.,* 1994; Jachmann, 2002).

Waterhole counts are usually done to collect data on population demographics (gender and sex ration), of various species which are not easily obtained by other sampling methods. This method is usually done on full moons during the dry season and requires many observers for a continuous period of (24-48 hours) (Chapter 2). The counts are done from hides overlooking the waterholes and the method assumes that each animal would come to drink at the waterhole at least once a day, therefore all animals can be counted in a given day. The challenge with this method is that the assumption isn’t true for some species that are not water dependend e.g. kudu (*Tragelaphus strepsiceros*).

1.2. The Waterberg National Park

The Waterberg National Park (WNP) is situated in northern Namibia, approximately 68 km south east of the town of Otjiwarongo. It is a wedge-shaped plateau, and the periphery is made of up near vertical cliffs, up to 300m high on the north-western side, details in chapter two. The plateau lies between 1550 and 1850 m above sea level, and between 100 to 300 m above the surrounding plains. It is fenced on the north-eastern side. The Waterberg is 40,500 ha in extent, of which 40,000 ha situated on the plateau. The top of the plateau is made up of lithified dunes, known as aeolianite (Erb, 1993). More than 90% of the rainfall occurs from October to March. Most (77%) of the rain falls between December and March, with February being the wettest month (Erb, 1993). Perennial water is found only in natural springs and artificial boreholes and the distribution of animals in the park is strongly influenced by the positions of these permanent water sources, details in chapter three. The first human inhabitants of the Waterberg were the San people, living their traditional lifestyle on the plateau. The Waterberg was the site of one of the major turning points in Namibia's history, specifically for the Herero tribe who at that time inhibited the area. In 1904, the Herero people lost their last and greatest battle against the German Colonial forces in the Herero and Namaqua wars, where the Herero people lost nearly two thirds of their population as a result of the war.

The Waterberg Plateau National Park was proclaimed a rare and endangered game species sanctuary in 1972 by the then government of Namibia. The park has played a vital role in breeding species for the restocking of other parks and conservation areas with Namibia’s most rare and valuable game species. As the plateau is mostly inaccessible from beneath, several of Namibia's endangered species were relocated here starting from the early 1970s into the 1990s to protect them from extinction due to predators and poaching (Du Preez, 2001 unpublished). These species included a variety of ungulates of different sizes, namely the white rhino (*Ceratotherium simum*), black rhino (*Diceros bicornis*), buffalo (*Syncerus caffer*), eland (*Tragelaphus oryx*), roan antelope (*Hippotragus equinus*), sable (*Hippotragus niger*), giraffe (*Giraffa camelopardalis*), red hartebeest (*Alcephalus buselaphus*), kudu (*Tragelaphus strepsiceros*), gemsbok (*Oryx gazella*), duiker (*Sylvicapra grimmia*), steenbok (*Raphicerus campestris*), klipspringer (*Oreotragus oreotragus*). The Park also houses two large to medium-size carnivores, the Leopard (*Panthera pardus*) and the Side-striped jackal (*Canis adustus*) and a large number of bird species of which the most important for conservation is the Cape vulture (*Gyps coprotheres*) which is a rare and endangered species.

The park has seven water holes, namely: Duitsepos, Kiewit, Elandsdrink, Geelhout, Heilboom, Secridata, and Bergtuin, which are evenly distributed across the plateau. They serve as the main water supply for the animals throughout the year, with exception of a few natural pans that normally dry up soon after end of the rainy season. Water is pumped from the canal which runs across the north-central parts of the country from the Berg Aukas and Kombat, where it is then diverted to the seven waterholes in WNP, details in chapter two. Three of these waterholes have hides (shelters used to observe wildlife at close quarters), namely Hielboom, Duitsepos and Bergtuin. Besides the seven waterholes, on the plateau there is a ‘vulture restaurant’ that serves as a feeding station for vultures on detected dead game in the park. Due to the fact that there are no scavengers on the plateau, the dead carcasses are dragged to the vulture restaurant where tourist/researchers get the opportunity to view, identify and monitor the different species of vultures and other birds of prey breeding on the plateau.

Figure 1.1 Vulture Restaurant Hide

Figure 1.2 Giraffe carcass and Buffalo skull at the Vulture Restaurant

The park also has a boma (local traditional name for an enclosure) used to secure and protect wildlife. The boma is used to facilitate and quarantine animals that are being translocated out of the park or animals being introduced in to the park. Before any of the animals are translocated or introduced into the park, they are kept at the boma and tested for diseases.

Figure 1.3 Buffalo in the Waterberg boma

1.3. Rationale

The park supplies other conservation areas and as well as community conservancies in Namibia with economically highly valuable species such as rhino, eland, roan antelope and giraffe. It is therefore crucial to understand the ecological aspects of species in WNP and the factors that drive them in order to ensure long term viability of the park to serve as a breeding station for all other conservation areas in Namibia and beyond. It is also of paramount importance to regulate population sizes of species that show population growth beyond or those approaching the maximum ecological capacity of the park through harvesting of animals by means of game capture. Effectiveness of such an approach depends on accurate and updated data on population sizes of the park, including the demographic profiles of species (age classes and sex ratio) in order to allow objective assessment of harvesting rates.

It is therefore essential to embark on studies that will allow us to understand the impact that ungulate species have on each other and on the ecology of the park. These studies include the daily activities patterns of species, which may have a high survival value for any animal species and may be affected by a number of factors e.g. feeding, drinking, temperature, humidity, predators, competitors, biological cycle and other factors (Wakefield, 2006; Kanda, Cote, 2012). Water requirements and its availability may also greatly affect the diurnal activity pattern of wildlife and the effective management of both water resources and the animals depends on the knowledge of such patterns.

Secondly, the distribution and abundance of organisms is primarily determined by habitat types and availability. Hence, most efforts towards conservation are targeted towards studies on species habitats. Aarts *et al*. (2013) noted that if most animals were to move randomly in space, the use of different habitats would be proportional to their availability. However, this is seldom if ever the case. The processes that drive habitat selection and/or the suitability of habitat patches by wild ungulates are essential in providing insights into population dynamics, community structures and the functioning of ecosystems (Muposhi *et al*., 2016). One of the major determining features of habitat selection in a semi-arid country like Namibia is rainfall which intern provides primary production/biomass. Variation in precipitation determines the biomass of plant material and indirectly the carrying capacity of the ecosystem in which the ungulates occur and hence their distribution (Maron & Crone, 2006). Understanding habitat selection in ungulates and the processes that drive selection across fine to intermediate spatial and temporal scales is therefore vital in the conservation and management of species.

Thirdly, the interplay of numerous, often widely variable, environmental factors reflects the relative rates of natality and immigration versus mortality and emigration that determines the population of ungulates, as noted by Mason (1990). Age- and sex-specific vital rates and population dynamics are associated with density of the population (Gillard *et al*., 1998; Gillard *et al*., 2000; Mysterud, 2002). Prime-aged individuals have a higher survival rate than older individuals and juveniles within a population (Gaillard *et al*., 2000; Holand *et al*., 2002) and males frequently have lower survival rates than females (Clutton-Brock *et al*., 1997; Holand *et al*., 2002). It is therefore essential to understand whether apparent changes in adult survival at high density are due to density dependence in survival, or to changes in age structure.

Fourthly, population dynamics can be used to detect trends of species of special conservation concern over time. In the view of wildlife conservation it is empirical to have knowledge of population changes through long-term monitoring. For instance, there are a number national parks and game reserves in southern Africa, where long-term monitoring programs on entire ungulate assemblages could have been initiated, but only a few conservation areas have actually done so (Caro, 2008). Waterberg National Park is one of the few parks that have a database of ungulate assemblage over a period as long as 33 years. Therefore, proper sampling methods are crucial to facilitate wildlife conservationists to develop and implement nature conservation strategies, mitigate human wildlife challenges that will allow effective wildlife management (Ranson *et al*., 2012).

1.4 Aims

The management and conservation of species is mainly based on the understanding of the ecological aspects of particular species and the factors driving them. Hence, understanding species ecology provides insights into how best to manage and conserve the species, especially in a semi-arid country like Namibia with its irregular rainfall which is the key to primary production and the survival of these species. Thus, the aim of this thesis is to assess the factors driving the ecological aspects of ungulates in WPN, using different methods of ungulate sampling and generate information towards improved management and conservation of ungulate species in the Waterberg National Park, Namibia.

1.5 Objectives

The study objectives were:

- To investigate the daily drinking activity pattern of ungulates in the Waterberg National Park in Namibia.
- To assess the distribution and habitat use of ungulates across small to intermediate temporal and spatial scales, in Waterberg National Park, Namibia.
- To assess how population structure differs among species in the Waterberg National Park, Namibia
- To determine population trends of all ungulate species in the Waterberg National Park across the last 33 years (1980-2013), and to compare the populations trends with those over similar period in other regions of sub-Saharan Africa.

1.6 Outline of thesis

This thesis comprises of six chapters, adopting the manuscript format. It has a general introduction to the study (Chapter 1), four research chapters (Chapters 2-5) and a general conclusion and recommendations (Chapter 6). Four of the six chapters were prepared in a peer-reviewed publication format. Chapter 2 is published in a peer-reviewed journal, chapter 3 has been submitted to peer-reviewed journals, chapter 4 has been accepted for publication in a peer-reviewed journal and chapter 5 will be submitted soon.

Chapter 1, 'General Introduction' provides an introduction to the ecology of ungulates of Waterberg Plateau National in Namibia, and the justification for the study.

Chapter 2 examines the daily activity patterns of ungulates at water holes during the dry season in the Waterberg National Park, Namibia. This study was undertaken to determine whether larger ungulate species, as those less vulnerable to predation, would be more likely to be nocturnal in their drinking activity than the smaller species, that are more vulnerable to predation and to assess whether species of medium size would show any preference in that regard.

Chapter 3 describes the distribution, habitat use and abundance of ungulates in the park. Specifically, this was examined to determine habitat use by different species and assess whether general 1) animal densities decrease with increasing distance from the water points. I also investigated whether 2) small-bodied species are mostly confined to the immediate vicinity of the water points, and whether the 3) larger-bodied animals, particularly buffalo respond least to the distance from water.

Chapter 4 looks at the population structure of ungulates in the park. In this study we set off to determine 1) the relationship between species herd sizes and the four major vegetation types in WNP. I also investigated the 2) age and sex structure of species in W.N.P, and 3) the association between the field and water point census of herd sizes during wet and dry season of all species in order to find the most suitable sampling method.

Chapter 5 In an initial, descriptive step this study aimed: 1) to determine population trends of all ungulate species in the WNP over the last 33 years using aerial and waterhole counts and 2) to compare the population trends with those documented in other regions of sub-Saharan Africa. However, more importantly, the study aimed 3) to test the relationships between rainfall trends and the population dynamics of particular ungulate species, knowing that, due to water supplementation, these effects are primarily indirect, due to forage availability.

Chapter 6, ‘General conclusions and recommendations’ provides a brief analysis of the implications of the study outcomes and suggestions for future studies.

All pictures in the general introduction section have been taken by the candidate (Mr Evert Kasiringua).

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CHAPTER 2: DAILY ACTIVITY PATTERNS OF UNGULATES AT WATER HOLES DURING THE DRY SEASON IN THE WATERBERG NATIONAL PARK, NAMIBIA (PAPER 1)

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2.1 Abstract

In this study, daily drinking activity of all 12 herbivore species were conducted in the dry season at seven waterholes in the Waterberg National Park, Namibia, where only leopard (*Panthera pardus*) was present as a large carnivore. Drinking was more frequent between 15h00 and 22h00 than in the rest of the day. A conspicuous peak in drinking activity was in the evening between 18h00 and 19h00, when 15% of animals were recorded drinking water. Water holes had various frequency of attendance by particular ungulate species. Eland (*Tragelaphus oryx*) and buffalo (*Syncerus caffer*) were most frequently recorded species at water holes, comprising together almost half of all ungulates recorded. The kudu (*Tragelaphus strepsiceros*), roan (*Hippotragus equinus*), sable antelope (*Hippotragus niger*) and warthog (*Phacochoerus africanus*) were also in the group of water-dependent species (comprising together at water holes 41.2% of all animals recorded). Four groups of ungulates may be distinguished in the Waterberg National Park based on their daily drinking activity patterns: 1) evening and night drinkers: white rhino (*Ceratotherium simum*), black rhino (*Diceros bicornis*) and buffalo (i.e., those free of leopard predation risk); 2) night and morning drinkers: eland, gemsbok (*Oryx gazelle*) and kudu (i.e. those with limited leopard predation risk); 3) day drinkers: warthog, giraffe (*Giraffa camelopardalis*), roan, sable antelope, red hartebeest (*Alcephalus buselaphus*) (high leopard predation risk); 4) whole day and night drinkers: *dik-dik* (*Madoqua kirkii*), steenbok (*Raphicerus campestris*), common duiker (*Sylvicapra grimmia*). Most animals drinking during the night were more active in the first half (18h00–24h00) than in the second half (24h00–6h00) of the night.

Key words: *African ungulates, behaviour, daily activity, wildlife management*.

2.2 Introduction

Daily activity patterns are an important feature of biology of any animal species. They are affected by feeding and drinking, temperature and humidity, predators and competitors, biological cycle, moon phases and other minor factors (Aschoff, 1964; Wakefield & Attum, 2006; Hayward & Hayward, 2012; Kanda & Cote, 2012). In Africa, water requirement and its avail- ability may greatly affect the daily activity pattern of some animals. Effective management depends on the knowledge of such patterns (Winterbach & Bothma, 1998). This is especially applicable to larger ungulates (they have high economic value and high water requirements), such as elephant (*Loxodonta africana*), white rhino (*Ceratotherium simum*), black rhino (*Diceros bicornis*), plain zebra (*Equus quagga*), giraffe (*Giraffa camelopardalis*), buffalo (*Syncerus caffer*), eland (*Tragelaphus oryx*), gemsbok *Oryx gazella*, kudu (*Tragelaphus strepsiceros*), blue wildebeest (*Connochaetes taurinus*) and red hartebeest (*Alcephalus buselaphus*). Their general daily activity rhythm consists of alternating bouts of grazing and resting/ruminating (Winterbach & Bothma, 1998).

Drinking occupies merely a few percent of their daily activity budget (Rayn & Jordaan, 2005) and is often not even considered in budget calculations (e.g. Winterbach & Bothma, 1998; du Toit & Yetman, 2005; Regassa, 2014; Tahani & Ibrahim, 2014; Tekaling & Bekele, 2015). It is, however, one of the most essential activities in their life affecting all aspects of their biology, ecology and conservation (Hayward & Hayward, 2012). To date, studies on daily activity of African ungulates at water holes were conducted in the Hwange National Park, Zimbabwe (Weir & Davisen, 1960; Crosmary *et al*., 2012), Amboseli N. P., Kenya (Western, 1975), Etosha N. P., Namibia (du Preez & Grobler, 1977), and in Kruger N. P., South Africa (Thrash, 1998; Cain *et al*., 2012; Hayward & Hayward, 2012).

The aim of this study was to investigate the daily drinking activity pattern of ungulates in another important African conservation area, the Waterberg National Park (WNP) in Namibia. Drinking is a highly risky activity, as large predators tend to focus attention around major water holes (Crosmary *et al*., 2012). In order to avoid being preyed upon, ungulates should develop such activity patterns that enable them to minimize the predation risk (for example by avoiding nights when predators are most active). On the other hand, ungulates will also compete among themselves for a free access to water (especially during the day). It was predicted, therefore, that the larger ungulate species, as those less vulnerable to predation, should be more nocturnal in their drinking activity than the smaller species, more vulnerable to predation. Species of medium size should show no special preference in that regard. In this study, we test this hypothesis.

2.3 Study area

WNP is situated in the Otjozonjupa Region in northern Namibia, 280 km north of Windhoek and 68 km south east of Otjiwarongo, at the following coordinates: 20°25′S, 17°13′E (Fig. 2.1). WNP is 49 km long from south west to north east, and 8–16 km width. It is 40 500 ha in surface size, with 40 000 ha on the plateau and 500 ha in foothills. The plateau arises from 1550 to 1850 m above sea level and between 100 to 300 m above the surrounding bush plains. The periphery of the plateau forms almost a vertical cliff, up to 300 m high. The top of the plateau is made up of aeolianite (lithified dunes) of the Etjo Formation, which is ca. 200 million years old. The sandstone is covered with Kalahari sand (W. Hegenberger, unpubl. report). There are no permanent water courses or pans. The water is pumped into seven drinking holes (Fig. 2.1, Table 2.1), so it is freely available throughout the year.

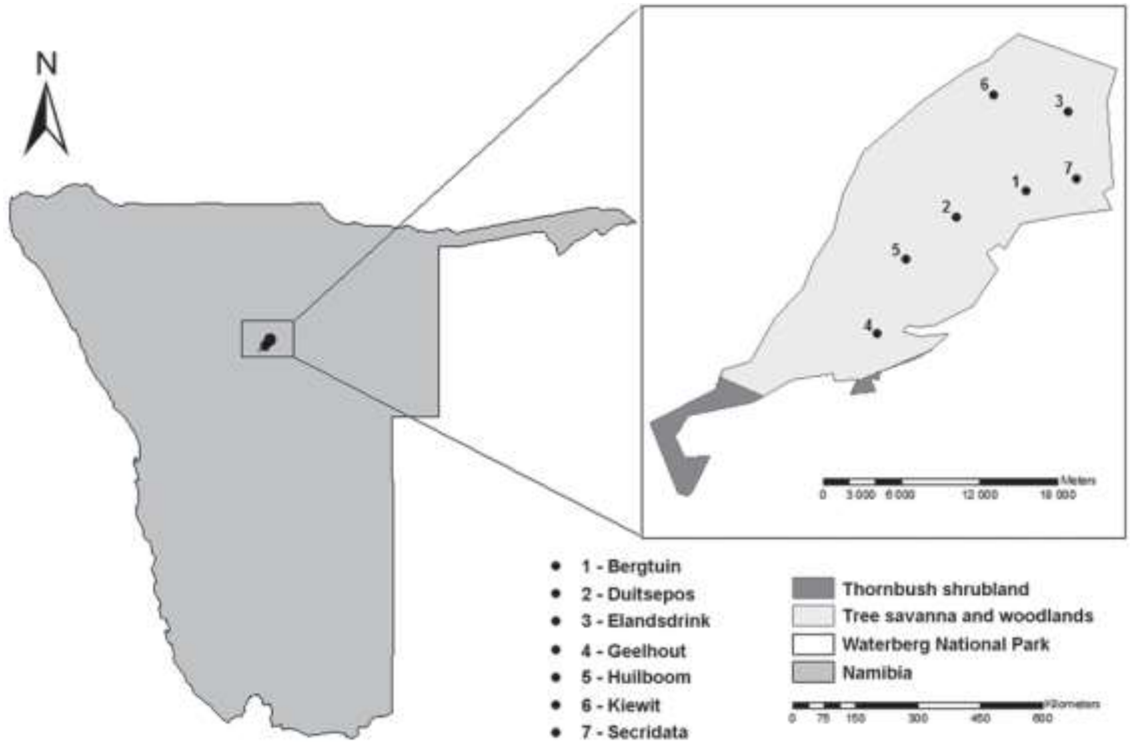

Figure 2.1. Location of the study area and distribution of waterholes (1–7) in the Waterberg National Park

Table 2.1. Location and elevation of the waterholes on the Waterberg National Park.

Water-Holes	Coordinates longit.	Coordinates latit.	Elevation
Bergtuin	20°22'45"S	17°21'14"E	1621m
Secridata	20°21'66"S	17°22'86"E	1598m
Elandsdrink	20°19'22"S	17°22'54"E	1621m
Kiewit	20°18'50"S	17°19'37"E	1647m
Duitsepos	20°23'57"S	17°18'16"E	1624m
Huilboom	20°25'47"S	17°15'69"E	1664m
Geelhout	20°28'56"S	17°14'64"E	1655m

The vegetation falls into the broad-leaf woodlands which are typical of the sandveld of eastern and north-eastern parts of Namibia (Mendelsohn *et al*., 2009). Three main vegetation communities within this type have been recognized: *Terminalia sericea–Melhania acuminata, Terminalia sericea–Blepharis integrifolia, Terminalia sericea–Thesium megalocarpum*, and *Peltophorum africanum* rock community (Jankowitz, 1983). Over 500 flowering plants and 140 lichen species were recorded in the WNP. Common trees include *Acacia ataxacantha, Burkea africana, Combretum collinum, C. psidioides, Dichrostachys cinerea, Grewia flavescens and G. retinervis, Lonchocarpus nelsii, Ochna pulchra, Peltophorum africanum, Terminalia sericea* and *Ziziphus mucronata*. Common grass species *are Andropogon schirensis, Brachiaria nigropedata, Digitaria seriata, Eragrostis jeffreysii, E. pallens, E. rigidior* and *Panicum kalaharense* (Jankowitz & Venter, 1987; Mendelsohn *et al*., 2009).

The plateau is divided into six burning blocks, each of which is burnt every 6–8 years. WNP falls into the ‘Hot Steppe’ climatic zone. The mean temperature is above 18 °C. More than 90% of the rainfall occurs from October to March. Average annual rainfall at Onjoka (below the Plateau) is 450.2±75.4 mm (Mendelsohn *et al*., 2009). The monthly variation of rainfall in the years of study is shown in Fig. 2.2. Among large carnivores, only leopard (*Panthera pardus*) is present in WNP. It reaches a density of 1 individual per 100 km^2 (Stein *et al*., 2011). This is rather low in comparison with 3.6 individuals per 100 km^2 in the neighbouring farms (Stein *et al*., 2011), but higher than in Etosha National Park (Stander *et al*., 1997). Other carnivore species, such as the cheetah (*Acinonyx jubatus*), spotted (hyaena *Crocuta crocuta*) or hunting dog (*Lycaon pictus*) appear in WNP only occasionally.

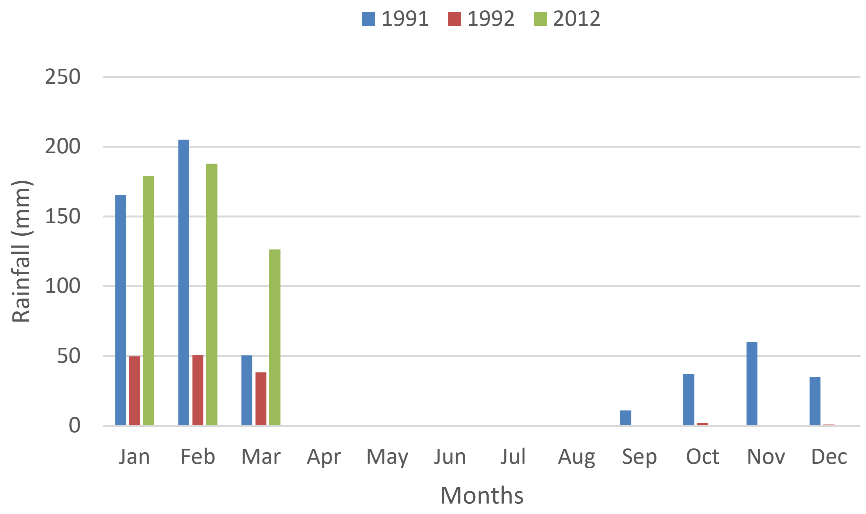

Figure 2.2. Monthly rainfall at Otjiwarongo in the years of study (data from hhttp://www.meteona.com/index.php/climate/seasonal).

2.4 Methods

Studies were conducted at seven waterholes in the WNP. Observations were conducted from specially constructed wooden shelter situated in a close proximity (ca. 50 m) to the water hole. Observations were carried out in the peak of the dry season, when the ungulates usually concentrate near water holes. The counts were organized around full moon nights to achieve greater visibility of the game during the night. Observations were aided with binoculars. Counts were conducted by a team of 2–4 observers, three times in dry season: June 1991, August 1992 and July 2012. At each water point, 2–3 observers counted animals visiting the waterholes for 48 hours, i.e. from 10h00 to 10h00 of the second following day in June 1991 and August 1992, and from 6h00 to 6h00 of the first following day in July 2012. Each animal coming to drink was timed, counted and identified to species level. Whenever possible, each individual was also sexed and aged, and identified individually (especially rhinos and giraffe) as to avoid double counting of some individuals which come more than once to the water point. The time of the sunrise and sunset in the month of study are presented in Table 2.2

Table 2.2. Sunrise and sunset time at Waterberg National Park in the month of study (data from https//www.timeanddate.com/sun/Namibia).

Date	Sunrise	Sunset	Day Length
1st June 1991	07:16	18:14	10:57:34
15th June 1991	07:21	18:14	10:53:05
30th June 1991	07:24	18:18	10:53:28
1st August 1992	07:18	18:30	11:11:28
15th August 1992	07:10	18:34	11:24:21
21st August 1992	06:57	18:38	11:41:15
1st July 2012	06:24	17:18	10:53:55
15th July 2012	06:24	17:23	10:59:38
31st July 2012	06:19	17:29	11:10:47

Animals were counted separately in each group. Since no year-to-year variations in the drinking activity were detected, the data from 1991, 1992 and 2012 were pooled and presented on graphs as from 6h00 to 6h00 of the following day. The $\chi 2$-test was used to test the differences in activity between day (6h00–18h00) and night (18h00–6h00) and between the first half (18h00–24h00) and the second half of the night (24h00–6h00). Its was predicted that the larger ungulate species, as those less vulnerable to predation should be more nocturnal in their drinking activity than the smaller species, more vulnerable to predation. Both number of animal groups and number of individuals were considered in the tests.

2.5 Results

All 12 ungulate species occurring in the WNP utilized water holes on a daily basis. During five day-and- night observations (24 hours), a total of 3519 animals were recorded. In addition to this number, animals from other orders were also recorded as utilizing water hole on a few occasions: springhare (*Pedetes capensis*) (n=1), scrub hare (*Lepus* saxatilis) (n=2), Cape porcupine (*Hystrix africaeaustralis*) (n=3), African wild cat (*Felis sylvestris lybica*) (n=1), black-backed jackal (*Canis mesomelas*) (n=6), bat-eared fox (*Otocyon megalotis*) (n=6), honey badger (*Mellivora capensis*) (n=4), brown hyaena (*Parahyaena brunnea*) (n=2), and Chacma baboon (*Papio ursinus*) (n=200) were relatively common at water holes. On the other hand, large carnivores, such as leopard and cheetah were recorded only on 1–2 occasions. Drinking by ungulates was more frequent between 15h00 and 22h00 (7 hours) than in the rest of the day

(24 hours). More than half of all individuals and groups were recorded during this time (Fig. 2.3).

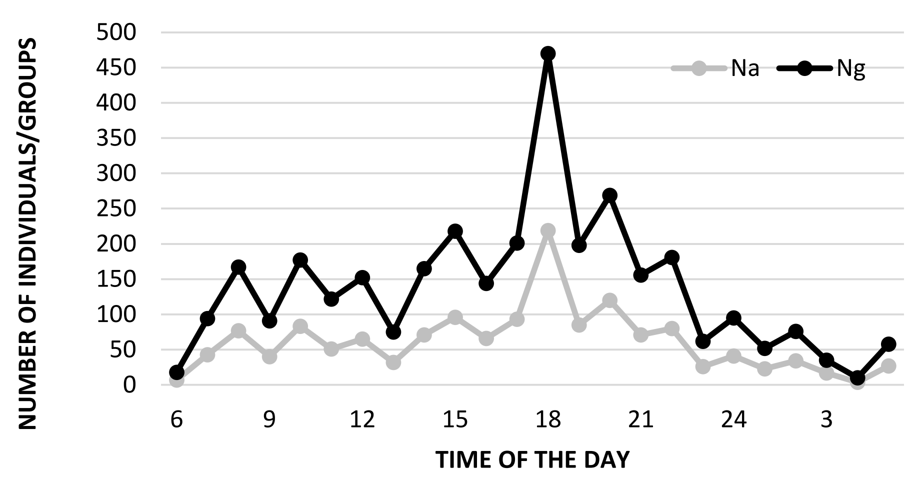

Figure 2.3. General daily drinking activity pattern of all ungulates in the dry season in the Waterberg National Park. Na—number of individuals, Ng—number of groups.

A conspicuous peak in drinking activity occurred in the evening between 18h00 and 19h00, when 15% of animals were recorded drinking water (Fig. 2.3). Water holes had various frequency of attendance by particular ungulate species. In one day (24 hours) the number of animals at a given water hole varied from 123 to 438 (mean=373; SD=117.8; n=7). The differences were caused mainly by the buffalo and eland, which were the most frequently, recorded species at water holes, comprising together almost half of all ungulates recorded. The kudu, roan, sable antelope and warthog were also in the group of water dependent species (comprising together 41.2% of all animals recorded at water holes).

All other ungulate species attended the water holes with lower frequencies (Figs 2.4–2.6). White rhino, black rhino and buffalo drank mainly between 18h00 and 24h00; eland between 18h00 and 24h00 and 6h00 and 9h00; warthog and giraffe mostly between 11h00 and 15h00; while kudu throughout the day and evening. Sable antelope and roan were found at water holes mainly between 7h00 and 15h00 (Fig. 2.4).

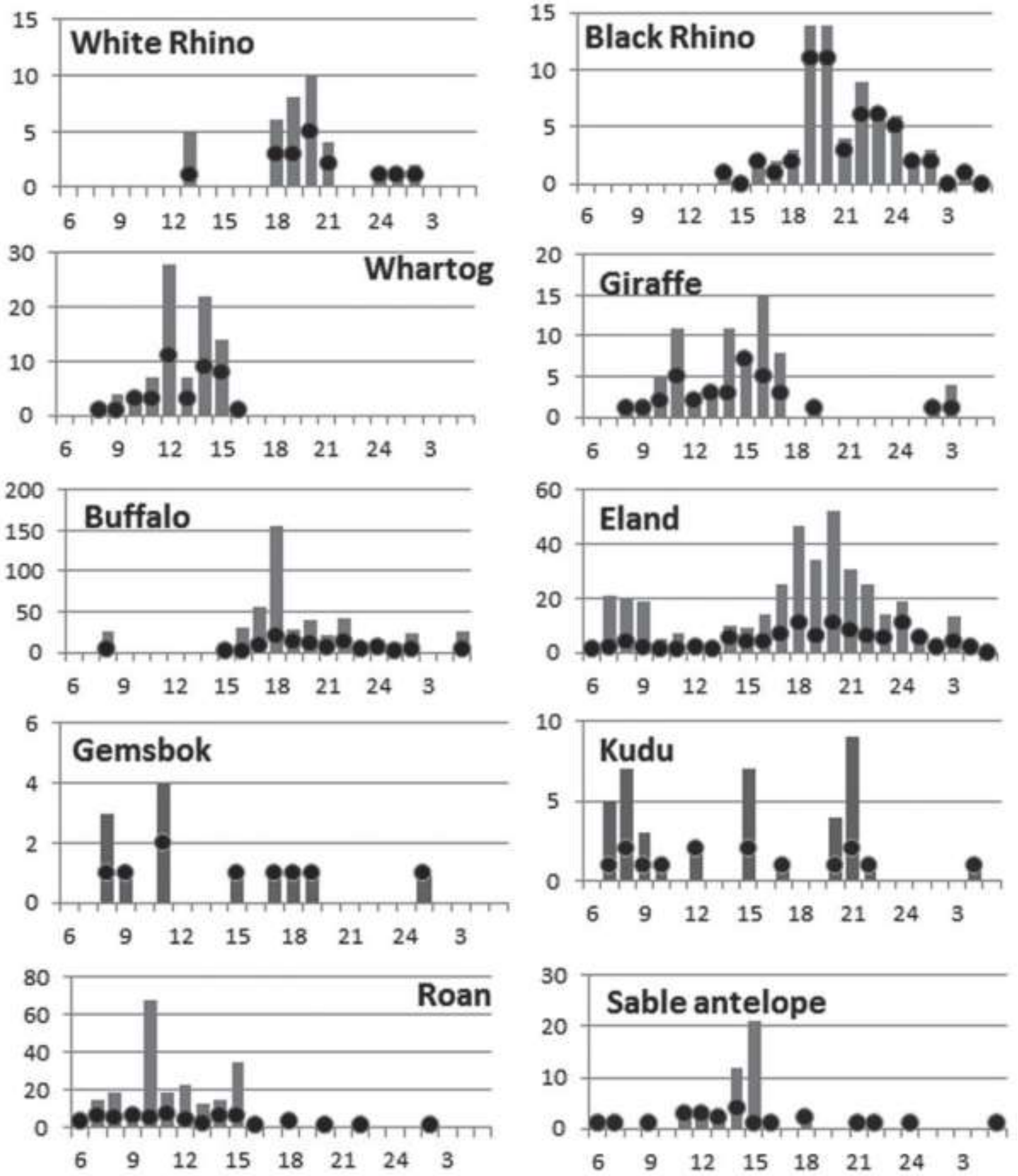

Figure 2.4. Daily drinking activity pattern of particular ungulate species in the dry season in the Waterberg National Park. Columns—number of individuals, dots—number of groups; x-axis—number of individuals/groups; y-axis—the time of the day.

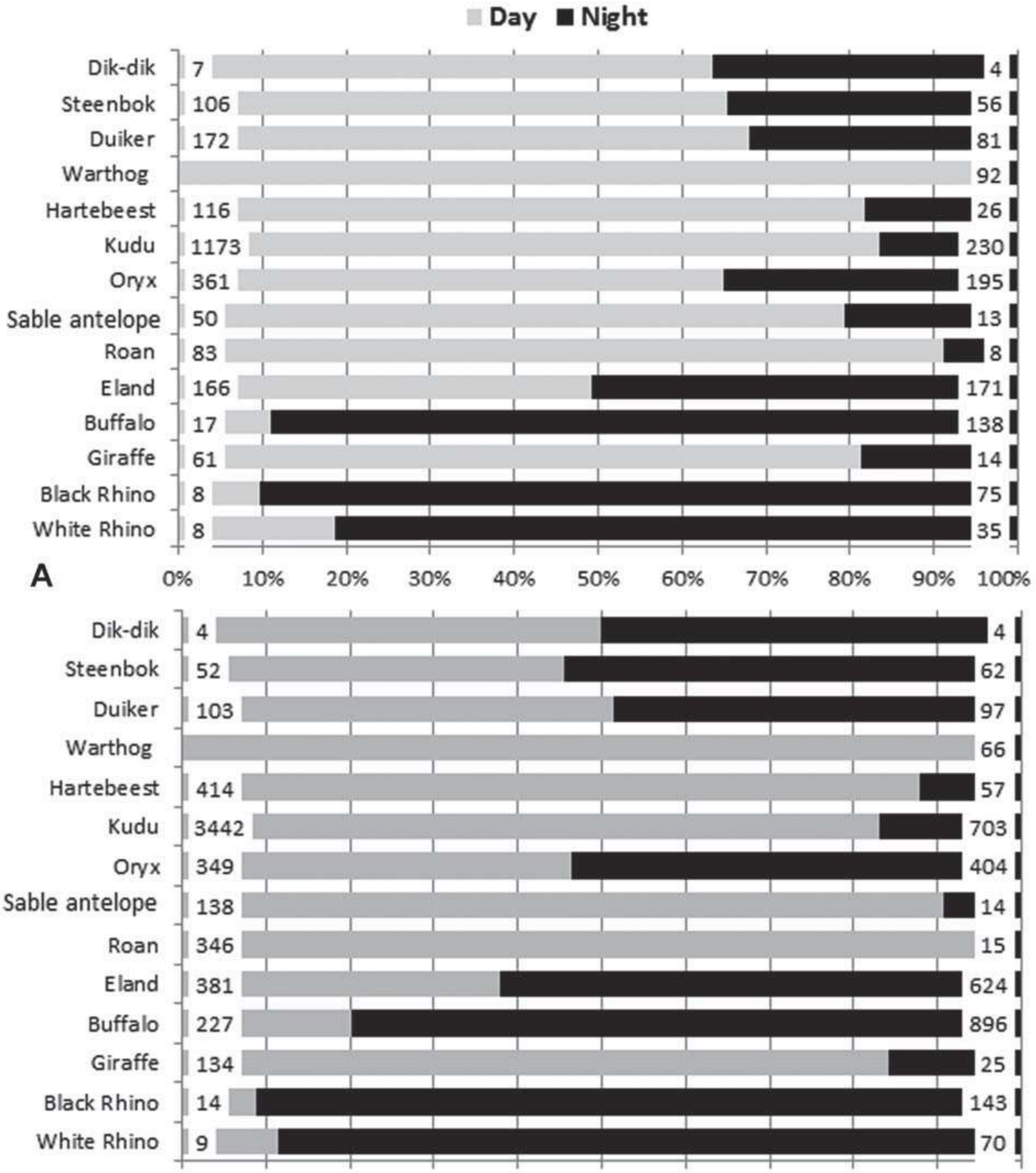

Figure 2.5. A—proportions (in %) of individuals of particular ungulate species visiting waterholes in the day and in the night in the dry season in the Waterberg National Park. At the extreme of each bars the total number of individuals is given. B—proportions (in %) of groups of particular ungulate species visiting waterholes in the day (6h00–18h00) and in the night (18h00–6h00) in the dry season in the Waterberg National Park. At the extreme of each bars the total number of groups is given

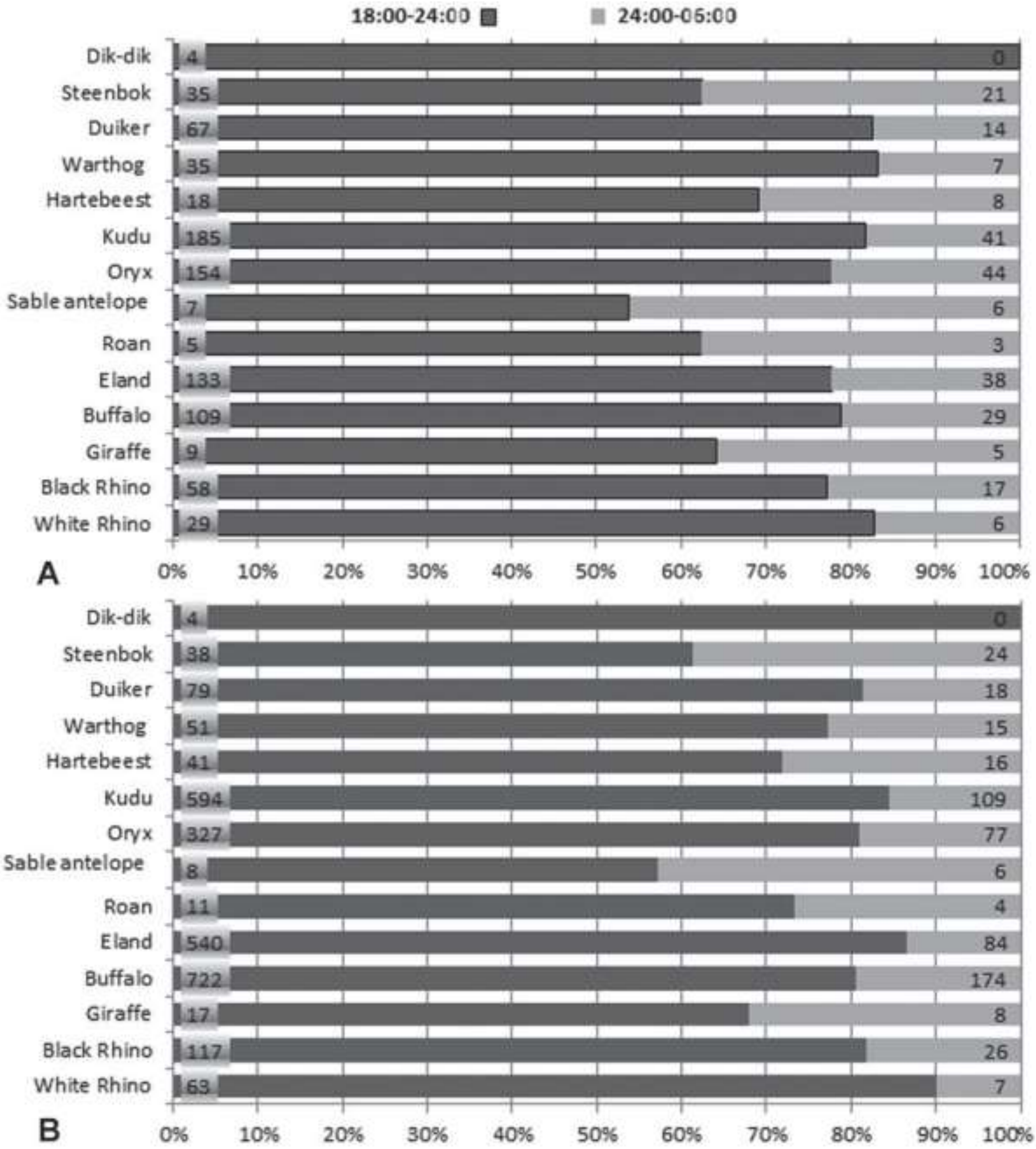

Figure 2.6. A—proportions (in %) of individuals of particular ungulate species visiting waterholes in the first (18h00–24h00) and in the second (24h00–6h00) half of the night in the dry season in the Waterberg National Park. At the extreme of each bars the total number of individuals is given. B—proportions (in %) of groups of particular ungulate species visiting waterholes in the first (18h00–24h00) and in the second (24h00–6h00) half of the night in the dry season in the Waterberg National Park. At the extreme of each bars the total number of groups is given.

Only the warthog was exclusively diurnal in its drinking activity. Mostly diurnal were roan, sable antelope, giraffe and red hartebeest (Fig. 2.5), and mostly nocturnal were buffalo, black rhino and white rhino. The eland was equally diurnal and nocturnal. Other ungulate species were mainly diurnal (Fig. 2.5). Most animals drinking during the night were more active in the first half (18h00–24h00) than in the second half (24h00–6h00) of the night (Fig. 2.6).

The difference between diurnal and nocturnal activities, both in relation to the groups and individuals visiting the water holes, were statistically highly significant (Table 2.3). Only four species, namely the steenbok, sable antelope, roan and giraffe were relatively active in the second half of the night (ca. 1/3 of night activity). These differences were statistically highly significant both in relation to groups and individuals (Table 2.3).

Table 2.3. Statistical analysis between daily and nocturnal drinking activity, and between such activity in the first (18h00–24h00) and second (24h00–6h00) half of the night. Degree of freedom =1. E<5—expected value lower than 5.

Ungulate species	Difference between day and night				Difference between the first and the second half of the night			
	groups		individuals		groups		individuals	
	x^2	p	x^2	p	x^2	p	x^2	p
White Rhino	17.0	0.01	47.1	0.01	15.1	0.01	44.8	0.01
Black Rhino	54.1	0.01	106.0	0.01	22.4	0.01	57.9	0.01
Giraffe	29.5	0.01	74.7	0.01	1.1	>0.05	3.2	>0.05
Buffalo	94.5	0.01	398.5	0.01	46.4	0.01	335.2	0.01
Eland	0.1	>0.05	58.8	0.01	52.8	0.01	333.2	0.01
Roan	61.8	0.01	303.5	0.01	E<5		3.3	>0.05
Sable	21.7	0.01	101.2	0.01	0.1	>0.05	0.3	>0.05
Gemsbok	49.6	0.01	4.0	0.05	61.1	0.01	154.7	0.01
Kudu	633.8	0.01	1809.9	0.01	91.8	0.01	334.6	0.01
Hartebeest	57.0	0.01	270.6	0.01	3.8	0.05	11.0	0.01
Tseseebe	1624.9	0.01	4336.8	0.01	18.7	0.01	19.6	0.01
Warthog	32.7	0.01	0.2	>0.05	34.7	0.01	38.4	0.01
Common Duiker	15.4	0.01	E<5		E<5		E<5	

2.6 Discussion

The utilization of water by game differs from habitat to habitat, from month to month and from species to species (Cain *et al.*, 2012; Crosmary *et al*., 2012; Hayward & Hayward, 2012). The drier the habitat, the higher the water demand. An increase in salt and protein content of vegetation causes an increase in water intake (Bothma, 2002; Hayward & Hayward, 2012). In the dry season, water intake from artificial holes is much higher than in the wet season (Cain *et al.*, 2012; Hayward & Hayward, 2012). The larger, the animal species the higher water intake (Hayward & Hayward, 2012). Among herbivores, grazers demand more water than browsers, and young animals more than adults. Water intake also increases during pregnancy (Bothma, 2002). These variations may influence the daily drinking activity patterns.

This study was based on observations carried out only in the nights with full moon. This could possible biased the results, as moon cycle may affect the circadian pattern of some mammal species. It is known that as the moon becomes darker, or it is closer to the new phase, there is often a higher frequency of movement of some animal species (Cozzi *et al.*, 2012; Pratas-Santia-go *et al.*, 2016). This aspect of activity of African ungulates has been, however, neglected by researchers. It is possible that diurnal or crepuscular species become more nocturnal under full moon nights, while predators are possibly more active when it is new moon. This premise requires, however, detailed investigation. Water requirements differ markedly from species to species, e.g. white rhino—72 litres per day, giraffe—40, black rhino—35, buffalo—31, eland—23, roan—10, sable antelope, gemsbok and warthog—9 litres (Bothma, 2002).

Drinking frequency, which is linked to the water requirement and drinking activity, differs from species to species, from habitat to habitat, and from month to month. It is also greatly influenced by distribution, and the number of water points. In dry season, ungulates drink water more frequently than in the wet season. If the water is freely accessible and evenly distributed, most ungulate species will drink at least once a day (Bothma, 2002; Cain *et al*., 2012; Crosmary *et al*., 2012; Hayward & Hayward, 2012). For example the elephant in Etosha National Park, where water holes are evenly distributed and easily accessible, frequents water once a day (du Preez & Grobler, 1977), in drier neighbouring Koakoland, where the water is not so freely available—every three days (Bothma, 2002), in Kruger National Park, South Africa, which is more humid than Etosha N.P., but where water is not so evenly distributed as in Etosha N.P., every second day (Bothma, 2002).

Four groups of ungulates may be distinguished in the WNP based on their daily drinking activity patters: 1) evening and night drinkers: white rhino, black rhino and buffalo; 2) night and morning drinkers: eland, gemsbok and kudu; 3) day drinkers: warthog, giraffe, roan, sable antelope, red hartebeest; and whole day and night drinkers: dik-dik, steenbok, common duiker. This grouping is interesting as it reflects to a large extend the risk of ungulates to leopard predation. Since this risk is low in the case of large herbivores such as rhinos and buffalos, they are the only which have main drinking activity in the night when the leopard predation is the highest.

The vulnerability to leopard predation is low in the case of large spiral-horned antelopes, such as the eland, gemsbok and kudu (Hayward *et al*., 2006; Hayward & Kerley, 2008; Crosmary *et al*., 2012), and it is why they are active in drinking both in the night and in the morning. The giraffe, roan, sable antelope, red hartebeest, and warthog are vulnerable to leopard predation (Hayward et al., 2006; Hayward & Kerley, 2008; Crosmary *et al*., 2012), and they are at water holes mostly in the day. The small antelopes, fall well within the preferred prey size of the leopard (Stander *et al*., 1997; Hayward & Kerley, 2008). They were, therefore, expected to be mostly diurnal in their drinking activity, but at WNP they were in fact equally active in the day and night. The sample size for those species was, however, too meagre to make a firm statement about their preferred time. They are also known to be quite independent of water in their territories (Kingdon, 1996).

The activity pattern of African ungulates at waterholes in dry seasons may be affected also by megaherbivores, such as elephant, white rhino, black rhino, buffalo, and eland. If those megaherbivores occur in a given area in larger numbers, then they tend to dominate at waterholes in the evening, between 18h00 and 21h00. This appears to be most preferred time for drinking activities for most ungulates (Weir & Davisen, 1960; du Preez & Grobler, 1977; this study), but megaherbivores may easily compete with smaller species, eliminating them from waterholes in that time. Night, especially the second half, is generally avoided by most herbivores (Weir & Davisen, 1960; du Preez & Grobler, 1977; Canda & Cote, 2012; Hayward & Hayward, 2012; this study). Large predators, such as the lion *Panthera leo*, leopard, and spotted hyaena are most active in that time, as has been shown by du Preez & Grobler (1977) and by Hayward & Hayward (2012). As anti-predator adaptation, medium-sized and small ungulates avoid drinking water at that time, even in the areas where their density of those predators is very low (e.g. in WNP). The Warthog was exclusively diurnal in drinking activity in all three study areas (Appendex 1). Among African ungulates, it is one of the most vulnerable species to large carnivore attacks.

The daily drinking activity patterns of ungulates in the WNP are quite different from those in Etosha N.P., but similar to those in Wankie N.P. In Etosha N.P. and WNP despite the relatively short distance between these areas, only the warthog shows the same activity pattern. On the other hand, there were five ungulate species with the same daily activity patterns in the WNP, and Wankie N.P., Etosha N.P. is an arid environment, while the vegetation in WNP and Wankie N.P. has similar structure of wet savanna and more humid climate. Probably, the density of large predators, such as lion, leopard, cheetah, hunting dog and spotted hyaena may play a role in this regard (Kanda & Cote, 2012). Their densities are much higher in Etosha N.P. than in WNP. In conclusion, this study found that larger ungulate species, were more nocturnal in their drinking activity than the smaller species which are more vulnerable to predation as predicted. Any disturbances at waterholes linked to their repair, reconstruction, enlargement etc. should be avoided in late afternoon and at evenings. In the dry season, they should take place, if possible, in the night, preferable in the second half of the night. On the other hand, tourists are encourage to visit specially constructed observatory points near the waterholes in late afternoon and evenings, but only in a way to avoid any disturbances of the game.

2.7 Acknowledgements

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Appendex 2.1. Comparison of daily drinking activity of ungulates in three areas in Africa.

Place	Pattern of activity				Source
	Evening/night	Night/morning	Day	Day/night	
Wankie N.P., Zimbabwe	Buffalo, Giraffe, Zebra	Eland, Blue Wildebeest	Warthog Kudu, Sable, Roan		Weir & Davisen 1960
Etosha N.P., Namibia		Black Rhino, White Rhino, Elephant	Warthog, Kudu, Gemsbok, Eland	Giraffe	Du Preez & Grobler 1977
Waterberg P.N.P., Namibia	Black Rhino, White Rhino, Buffalo	Eland	Warthog, Giraffe, Sable, Roan	Kudu	this study

CHAPTER 3: DISTRIBUTION, HABITAT USE, AND ABUNDANCE OF UNGULATES IN WATERBERG NATIONAL PARK, NAMIBIA (PAPER 2)

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3.1 Abstract

Understanding habitat selection by wild ungulates is essential for adaptive ecosystem management and wildlife conservation in semi-arid savanna ecosystems. We here make an attempt to characterize the habitat preferences and habitat use of twelve ungulate species in Waterberg National Park, Namibia, with data collected twice a year during both the wet season (February to April) and dry season (June to August) of the year 2015 and 2016. Data were collected using distance sampling method from road counts. The detection probability of ungulate decreased with increasing distance from the transect for all species. Buffalo and eland were most frequently recorded species, comprising together more than half of all ungulates recorded. The probability of occurrence in large ungulates was mostly influenced by distance from the water holes, whereas distance from roads explained much of the variation in medium-sized herbivores. Predictions did not significantly differ annually or seasonally. We conclude that large herbivores may not necessarily utilise larger habitat patches over medium sized herbivores due to the habitat homogenizing effect of water provisioning.

Key words: *African ungulates, body mass, browsers, grazers, wildlife management*

3.2 Introduction

Habitat is a primary determinant of the distribution and abundance of organisms and is the target for most conservation efforts. It has been suggested that if animals moved randomly in space, the use of different habitats would be proportional to their availability (Aarts *et al*. 2013). It is essential to understand the processes driving habitat selection and/or the suitability of habitat patches by wild herbivores, as these provide insights into the processes driving population dynamics, community structure and the functioning of ecosystems (Muposhi *et al*. 2016).

An understanding of these patterns and processes is also critical for adaptive management, particularly towards ecosystem management and wildlife conservation. This has been pointed out across a range of ecosystems, including semi-arid savanna (Muposhi *et al*. 2016). Bukombe *et al*. 2016 suggested that detection of individual animals and estimation of ungulate population density might be a function of vegetation cover, animal size (body size), observation distance or season (Boyce 2016). Boyce & McDonald (1999) recognized that resource selection functions (RSF) can be used to map the probability for the use of various habitats by different species and by summing up these probabilities, population size could be estimated.

In savanna ungulates, body mass drives habitat selection in a way that allows for species coexistence (Cromsigt *et al*. 2009). Large species use a larger proportion of the landscape than smaller species, because of a wider food and habitat quality tolerance, which allows the large species to forage across diverse habitat types (Muposhi *et al*. 2016). This means that, as long as the overlap in potential resource use is incomplete, species can coexist even if there are overlaps in their fundamental niches (Putman 1996; Makhabu 2005). Individual species can occupy different and non-overlapping post-interactive niche in the presence of the other potentially competing species (Putman 1996). Hence, large-bodied browsers are more evenly distributed over the landscape than small ones.

In African semi-arid savanna, smaller-bodied species such as the duiker (*Sylvicapra grimmia*) and steenbok (*Raphicerus campestris*) have a variety of range sizes whereas large bodied species like eland (*Tragelaphus oryx*) and buffalo (*Syncerus caffer*), have only large ranges. This suggests that high habitat heterogeneity facilitates diverse assemblages of different-size ungulates (Aava 2001). Other factors intrinsic to the animals, such as digestive physiology further influence habitat selection, with ruminants having a wider diet tolerance than non-ruminants of the same size (Cromsigt *et al.* 2009).

In parallel, environmental factors, such as variations in precipitation, affect the production of plant material and indirectly the carrying capacity of the ecosystem in which these animals occur (Coe *et al.* 1975). Spatial and temporal variation in water availability affects the distribution and habitat use of different species in multiple ways (Epaphras *et al*. 2007). It has been suggested that water utilization of ungulates differ from habitat to habitat, from month to month and from species to species (Cain *et al*. 2012; Crosmary *et al*. 2012; Hayward & Hayward 2012). Animals drink more regularly during the dry season in order to meet their body requirements of water. Epaphras *et al.* (2007), suggest that animal daily and seasonal migrations are to a degree determined by spatial and temporal surface water distribution.

Water necessities are said to generally scale with body size (du Toit 2002; Brown 2006), however some species are more or less independent of surface water e.g. klipspringer (*Oreotragus oreotragus*), although they are likely to drink when water is available. Browsers or mixed feeders e.g. red hartebeest (*Alcelaphus buselaphus caama)* and Oryx (*Oryx gazella)* are also more likely to be water independent (du Toit 2002), obtaining the bulk of their water from forage, especially in the wet season. Species adapted to arid environments, like the gemsbok, often have physiological adaptations to reduce sweating, store water, recycle water more efficiently, or reduce water losses in faeces and urine (Coughenour 2008). In some systems, most grazer species (e.g. zebra, *Equus quagga*) are associated with water points, whereas browsers and mixed feeders are indifferent to water points e.g. eland (Smit et al. 2007). Thus, differences in water requirements as mentioned above may cause animals of different species to distribute differently around the water points.

Mobility is another factor that can influence the distributions of species around water points, some species like elands, and roan antelope (*Hippotragus equinus*) walk long distances from the water points to feed whereas smaller species like the impala (*Aepyceros melampus*) preferably feed closer to the water points. This means that the source of water becomes the focus of grazing activity, which results in a zone of attenuated impact (a piosphere) around each water point (Lange 1969). Furthermore, the relationship between rainfall and soil nutrients may also have a role in the distribution of the animals, since rainfall promotes large plant biomass production and soil nutrients promotes high concentration of nutrients in the plant tissues (Olff *et al*. 2002). Previous studies have noted a relationship between annual rainfall and the large African herbivore biomass (Watson 1972; Leuthold 1973; Sinclair 1974; Coe *et al*. 1975). Phillipson (1975) indicated that elephant populations in the Tsavo National Park may have in fact been governed by temporal and spatial variations in primary production. If this is true then one can assume that the highest herbivore diversity should occur in locations with high nutrient content and intermediate moisture (Olff *et al*. 2002). As a result, the areas closest to the water are normally heavily grazed /browsed and may particularly in the dry season be more or less devoid of food, forcing animals to feed away from the water. Thus, the structure and function of the African savanna ecosystems are strongly influenced by the ungulate communities, e.g. composition of body size classes and feeding guilds (du Toit & Cumming 1999).

The aim of the present project is to increase the understanding of the habitat usage by ungulates across small to intermediate temporal and spatial scales, with data from the Waterberg National Park, Namibia. We specifically set off to determine habitat preference by different species and assess whether general 1) animal densities decrease with increasing distance from the water points. We also investigated whether 2) small-bodied species are mostly confined to the immediate vicinity of the water points, and whether the 3) larger-bodied animals, particularly buffalo respond least to the distance from water.

3.3 Methodology

3.3.1 Study area

The study was conducted in Waterberg National Park which is situated in the Otjozonjupa Region in northern Namibia, 280 km north of Windhoek and 68 km south east of Otjiwarongo (20°25'S, 17°13'E; Figure 3.1).

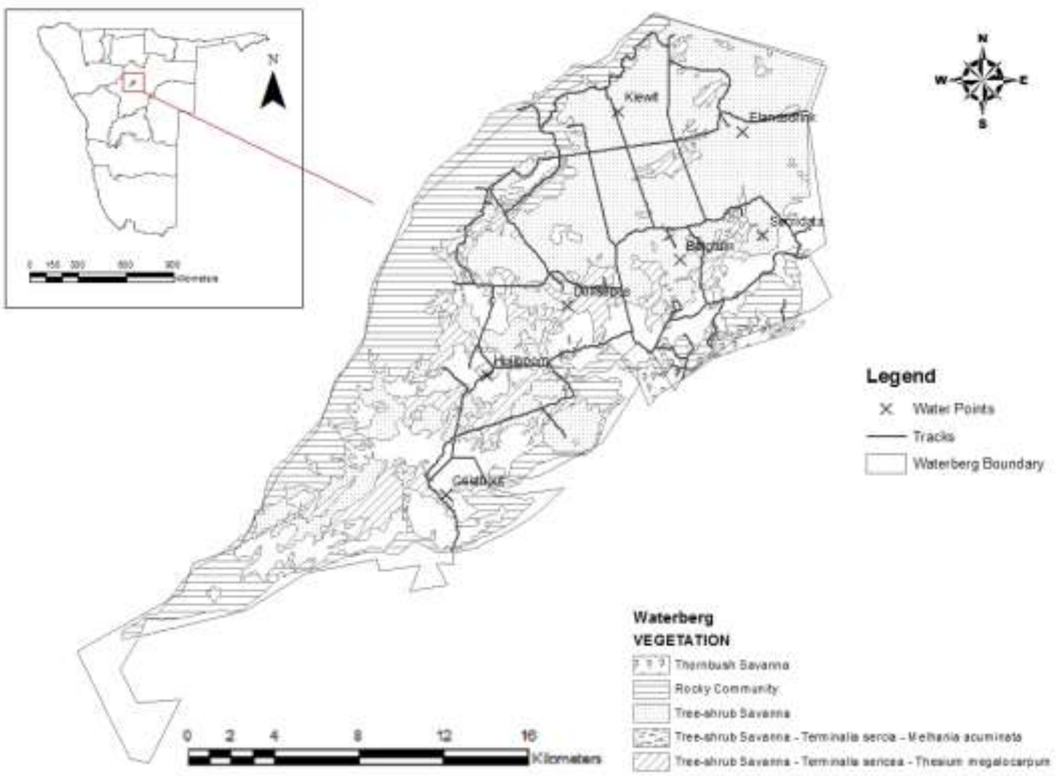

Figure 3.1. Waterberg National Park and the different vegetation types for in the park. Source: (Jankowitz 1983).

The WPN is 49 km long from south west to north east, and 8-16 km wide. It is 40,500 ha in size, with 40,000 ha on the plateau and 500 ha in the foot hills. The plateau arises from 1550 to 1850 m above sea level and between 100 to 300 m above the surrounding plain. The periphery of the plateau forms almost vertical cliffs, up to 300m high. The top of the plateau is made up of aeolianite (lithified dunes) of the Etjo Formation, which is ca. 200 million years old. The sandstone is covered with Kalahari sand (Hegenberger, 1990). There are no permanent water courses or pans. The water is pumped from the canal which runs across north central parts of the country from the Berg Aukas and Kombat mines where it is than diverted to the seven waterpoints in WNP (Figure 3.1), and is available throughout the year.

The vegetation falls into the broad-leaf woodlands which are typical of the sandveld of eastern and north-eastern parts of Namibia (Mendelsohn *et al*. 2009). Three main vegetation communities within this park have been recognized, with a fourth one occurring on rocky substrates: *Terminalia sericea-Melhania acuminate* covering 42% of the park, *Terminalia sericea-Blepharis integrifolia* covering 16% of the park, *Terminalia sericea-Thesium megalocarpum* covering 11% of the park, and the rock community *Peltophorum africanum* which covers 27% of the park (Jankowitz, 1983). Over 500 flowering plants and 140 lichen species were recorded in the Waterberg N. P. Common trees include *Acacia ataxacantha, Burkea africana, Combretum collinum, C. psidioides, Dichrostachys cinerea, Grewia flavescens* and *G.retinervis, Philenoptera nelsii, Ochna pulchra, Peltophorum africanum, Terminalia sericea* and *Ziziphus mucronata.* Common grass species are *Andropogon schirensis, Brachiaria nigropedata, Digitaria seriata, Eragrostis jeffreysii, E. pallens, E rigidior* and *Panicum kalaharense* (Jankowitz & Venter 1987; Mendelsohn *et al*. 2009).

The plateau is divided into 6 burning blocks, each of which is burnt every 6-8 years The Waterberg Plateau Park falls into the 'Hot Steppe' climatic zone. The mean temperature is above 18°C. More than 90% of the rainfall occurs from October-March. Average annual rainfall at Onjoka (below the plateau) is 450.2 ±75.4 mm (Mendelsohn *et al*. 2009). The total rainfall for Waterberg N. P. in the year 2015 was 142.7mm, of which less than half of that occurred in the months January to March with no rain in April, whereas in the year 2016 Waterberg National Park received a total of 404.4mm in rainfall, of which most of the years rain occurred in the months January, February, March and April (Figure 3.2).

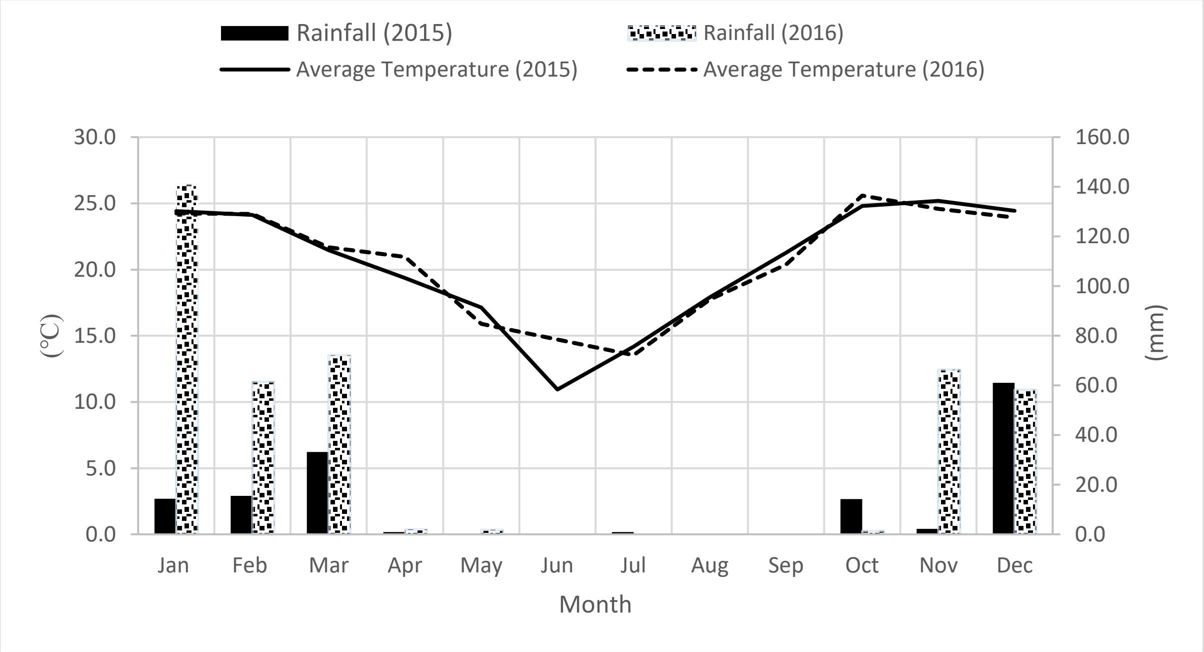

Figure 3.2. Rainfall of Waterberg N. P. for the years 2015 and 2016. Total rainfall for 2015 was 142.7mm and 404.4m in 2016. Source: (Sasscalweathernet.org/station_datasheet_we.php).

3.3.2 Data Collection

Data were collected using road counts during three months of Namibia's wet season starting in February to April of both 2015 and 2016, whereas the data for dry season were collected during the months of June to August for both years. A Toyota truck was used to drive along the transects, at a speed between 15-20km/hour. The sampling was started every day at 06:00am, with the odometer set to 0 at the starting point. Animals where observed from the vehicle by two individuals using binoculars. Observed animals were recorded using Global Positioning System (GPS) to plot the coordinates of the observation spot, and distance was estimated between 0 and 100m using a Nikon ACULON laser range finder for accuracy of identifying the sexes of the observed animals (0 if the observation was on the road). Coordinates of the seven (7) waterpoints were collected in order to determine animal vegetation preferences and estimate the distance between each point of observation and the nearest waterpoint. The total distance of transect covered per day varied between 50 and 70km. We avoided recounting of the animals by not returning along the same transects. Data of rhino occurrence are omitted from this study, merely because of the current poaching threats in Namibia.

3.3.3 Processing of GIS data

ArcGIS 10.x software was used to process the coordinates of the observed animals. A total of 52 attribute fields were added to the existing attributes for species observed in 2015 and 2016 representing wet and dry seasons respectively. Data were then populated/entered for each point of observation. Different symbols were used to represent the wet and dry season on the map, the observed points were then labelled according to the total number of species observed. The vegetation was categorized based on each vegetation type and displayed using a unique color ramp representing the different vegetation types. A transparency of 50% was applied on each vegetation color, in order to aid visualization of other overlaid data.

3.3.4 Statistical analyses

Data on habitat preference and habitat were not normally distributed but met the assumptions of Chi-square test for association using IBM SPSS version 20. Non-parametric Chi-square tests of association were, therefore, performed to determine if a particular animal species is associated with certain habitat or not (symbolizing usage or preference) and in which season (dry or wet) across the years 2015 and 2016. Secondly, one-way analyses of variance (ANOVAs) followed by post-hoc using Duncan's multiple range test at 5 % significant level tests were conducted to ascertain if the average distances to the water point differ among different species, seasons, years and season by species interactions, after testing for normality. Lastly, animal densities for 2015–2016 were estimated using line distance methodology, implemented in the software Distance 7.2 (Kiffner *et al*. 2017). The model fitted five different detection functions to the data (Thomas *et al*. 2010; Kiffner *et al*. 2017). The conventional detection models (all with cosine expansion) describe detectability as a function of perpendicular distance: uniform, half-normal, negative exponential, and hazard rate. Half-normal key, k(y) = Exp(-y**2/(2*A(1)**2)), where k is number of sample and A is the i-th parameter in the estimated probability function Based on the Akaike's information criterion (AIC) score of each model and the visual fit of the detection function near the transect line and goodness-of-fit statistics, we selected the best-fitting detection model for species and used this model to estimate and species densities (Kiffner *et al*. 2017).

3.4 Results

The maps generated based on the animal observation coordinates in relation to the four major vegetations suggested different habitat preferences of species based on the season (wet and dry) across the two years (2015-2016). The smaller species such as the duiker and steenbok which were predicted to be found in the immediate vicinity of the waterhole were not confined by the distance to waterpoints but rather evenly distributed among the four vegetations across the two seasons. On the other hand the medium sized (kudu) and larger animals like buffalo responded least to the distance from the waterhole as predicted (Appendix 3.3-3.14).

The detection probability in the half normal model had an AIC value of 7187.1, with a chi square value of 2313.11, Df = 24 (p=0.000). Therefore, we reject the null hypothesis that the expected values are not different from the observed. The intercept value of the detection probability was 0.900656 and slope of -0.47.

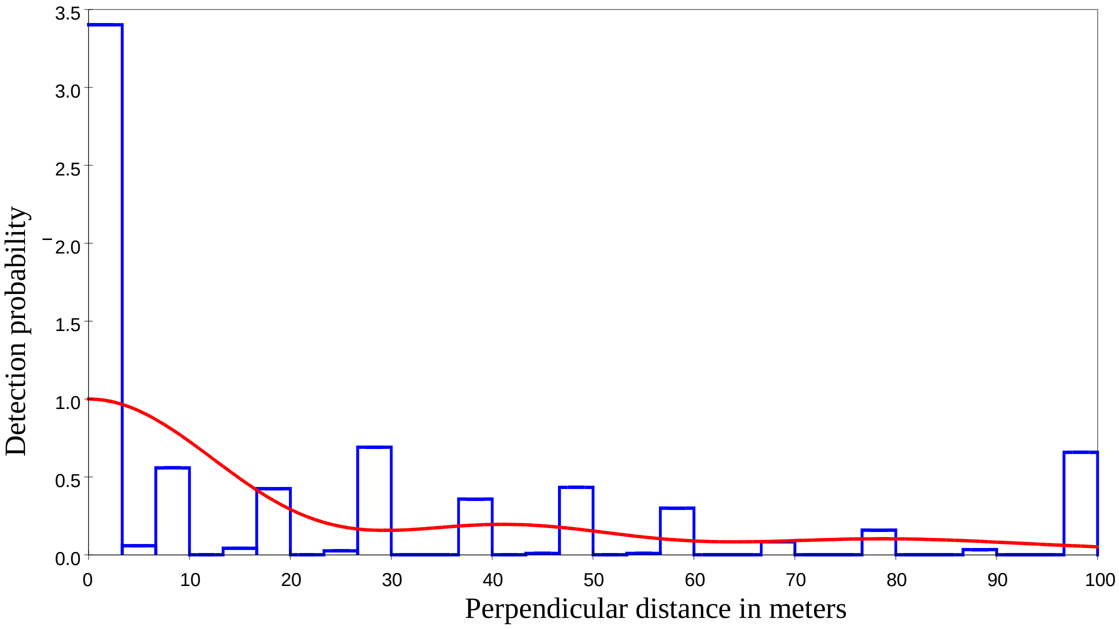

Figure 3.3. Detection probability in relation to perpendicular distance of ungulates in WNP.

The mean estimated density of animals (*D*) were 0.022293 per hectare with a 95% confidence interval of 0.020066 to 0.024767 animals per hectare, which translates to 963 (95% confidence interval 843 to 1040) animals in the survey area. The mean observed cluster size was 3.0988 animals (95%, CI, 2.74-3.60). The mean abundance (*N*) is 3745 animals (95%, CI, 3371 – 4161) in Waterberg National Park (Appendex 3.1). The Expected cluster size was 2.1722± 0.07 whilst the mean cluster was 3.0978± 0.19 (Appendix 3.2).

Different ungulate species showed diverse distribution patterns in relation to distance from the water points across the two years and between seasons. Buffalo avoided the Rocky community vegetation (*Peltophorum africanum*) during the wet season of 2015 and the tree shrub vegetation (*Terminalia sericea-Melhania acuminate*) during the dry season of 2016. Buffalo preferred the thorn bush vegetation (*Terminalia sericea-Blepharis integrifolia*) during the wet season of 2016 and the tree shrub (*Terminalia sericea-Thesium megalocarpum*) during the dry season of 2016. Giraffe (*Giraffa camelopardalis*) avoided the rocky community vegetation (*Peltophorum africanum*) during both years and seasons and preferred the tree shrub savanna (*Terminalia sericea-Melhania acuminata*) during the wet season of 2015, the thorn bush (*Terminalia sericea- Blepharis integrifolia*) during the dry season of 2015 and the tree shrub savanna (*Terminalia sericea-Thesium megalocarpum*) during the dry and season of 2015 (Table 3.1).

Eland preferred the rocky community vegetation (*Peltophorum africanum*) in both the dry and wet season in 2016 whilst avoiding it in the wet season of 2015. In the wet season of 2015 the eland avoided the tree shrub savanna (*Terminialia sericea-Therium megalocarpum*) whilst preferring it in the wet season of 2016. The oryx preferred the tree shrub savanna (*Terminialia sericea-Therium megalocarpum*) in the dry season of 2015 and the tree shrub savanna (*Terminalia sericea-Melhania acuminate)*. Sable (*Hippotragus niger*) strongly preferred the thorn bush (*Terminalia sericea-Blepharis integrifolia)* during the wet season of 2015 and 2016 and avoided the tree shrub savanna (*Terminialia sericea-Therium megalocarpum)*. Kudu (*Tragelaphus strepsiceros*) avoided the rocky community vegetation (*Peltophorum africanum*) during the wet season of 2015 and 2016, whilst they preferred the thorn bush (*Terminalia sericea-Blepharis integrifolia*) during the wet season of 2015 and the (*Terminalia sericea-Melhania acuminate)* during the wet season of 2016 (Table 3.1).

Roan antelope avoided the tree shrub (*Terminalia sericea-Melhania acuminate)* during the wet season of 2016 and rocky community (*Peltophorum africanum*) during the wet season of 2015 whilst preferring the thorn bush vegetation (*Terminalia sericea-Blepharis integrifolia)* during the wet season of 2016 and the tree shrub savanna (*Terminialia sericea-Therium megalocarpum*) during the dry season of 2015. The red hartebeest preferred the thorn bush during both wet and dry season 2015 whilst avoiding both the rocky community vegetation (*Peltophorum africanum*) and the tree shrub savanna (*Terminalia sericea-Melhania acuminate)* particularly during the dry season of 2015 (Table 3.1).

The duiker, steenbok and klipspringer didn’t show any statistical preference or avoidance to any habitat throughout both years. The most preferred vegetation over the two years was the thorn bush (*Terminalia sericea-Blepharis integrifolia),* followed by the tree shrub savanna (*Terminalia sericea-Melhania acuminate*), whilst the most avoided was the rocky community vegetation *(Peltophorum africanum).* The different species showed more preference to the different vegetation’s during the wet season of 2016 than they did during the wet season of 2015 and more avoidance to the different vegetation’s in the dry season of 2015 than they did during the dry season of 2016 (Table 3.1).

Table 3.1. Differences, as indicated by Chi-square tests in habitat use by ungulate species between dry and wet season in Waterberg National Park during the years 2015-2016. One asterisk indicate p < 0.05 and the two asterisk p < 0.01. The underlined values indicate preference.

Vegetation	**Tree shrub savanna** *Terminalia sericea-Melhania acuminata*				**Rocky Community** *Peltophorum africanum*				**Thorn bush** *Terminalia sericea-Blepharis integrifolia*				**Tree shrub savanna** *Terminalia sericea-Thesium megalocarpum*			
Season	**Dry**		**Wet**		**Dry**		**Wet**		**Dry**		**Wet**		**Dry**		**Wet**	
Year →	**2015**	**2016**	**2015**	**2016**	**2015**	**2016**	**2015**	**2016**	**2015**	**2016**	**2015**	**2016**	**2015**	**2016**	**2015**	**2016**
Buffalo	0.95	11.92**	0.09	0.35	1.62	0.44	9.03**	1.75	3.55	0.09	2.25	12.55**	2.12	15.08**	2.09	0.31
Giraffe	0.57	0.07	26.82**	0.03	14.38**	14.10**	36.50**	10.74**	8.08**	2.36	-	0.96	4.12*	2.33	14.79**	6.84
Eland	1.47	7.85	-	0.89	1.07	11.99**	73.33**	12.41**	2.75	1.13	86.99	7.63	0.72	-	43.34**	9.66**
Oryx	3.98	-	0.66	4.09*	-	-	-	-	2.02	-	-	-	8.62**	-	-	-
Sable	0.85	0.38	2.49	-	-	5.40	1.84	-	-	-	7.25**	13.39**	-	10.81**	-	-
Kudu	0.49	1.54	0.37	13.27**	-	-	5.17*	6.73**	-	-	9.97**	-	-	-	-	0.25
Roan	0.73	0.25	2.24	6.11**	7.51**	0.02	13.63**	1.19	2.21	-	0.03	4.68*	5.26*	0.78	2.71	1.85
Duiker	3.15	-	0.33	0.12	-	-	2.97	-	-	-	0.02	-	-		0.05	-
Red Hartebeest	4.42*		1.99	0.08	11.75**		-	-	23.73**	-	6.22*	-	0.53	-	-	-
Klipspringer	1.27	-	-	-	-	-	4.99		-	-	-		-	-	-	
Steenbok	0.04	0.37	0.05	0.17	-	-	-	-	-	-	-	-	-	-	-	-

There was no correlation between body size and distances of animals from the waterholes for either year or season (Figure 3.4). The relationship between weight and distance in the dry season of 2015 is given by $y = -0.0659x + 10.244$ with an $R^2=0.0404$. The relationship between weight and distance in the wet season of 2015 is given by $y = -0.0596x + 8.0435$ with an $R^2=0.0759$. The relationship between weight and distance in the dry season of 2016 is given by $y = -0.0197x + 7.2551$ with an $R^2=0.0076$. The relationship between weight and distance in the wet season of 2016 is given by $y = -0.0448x + 5.612$ with an $R^2=0.0372$.

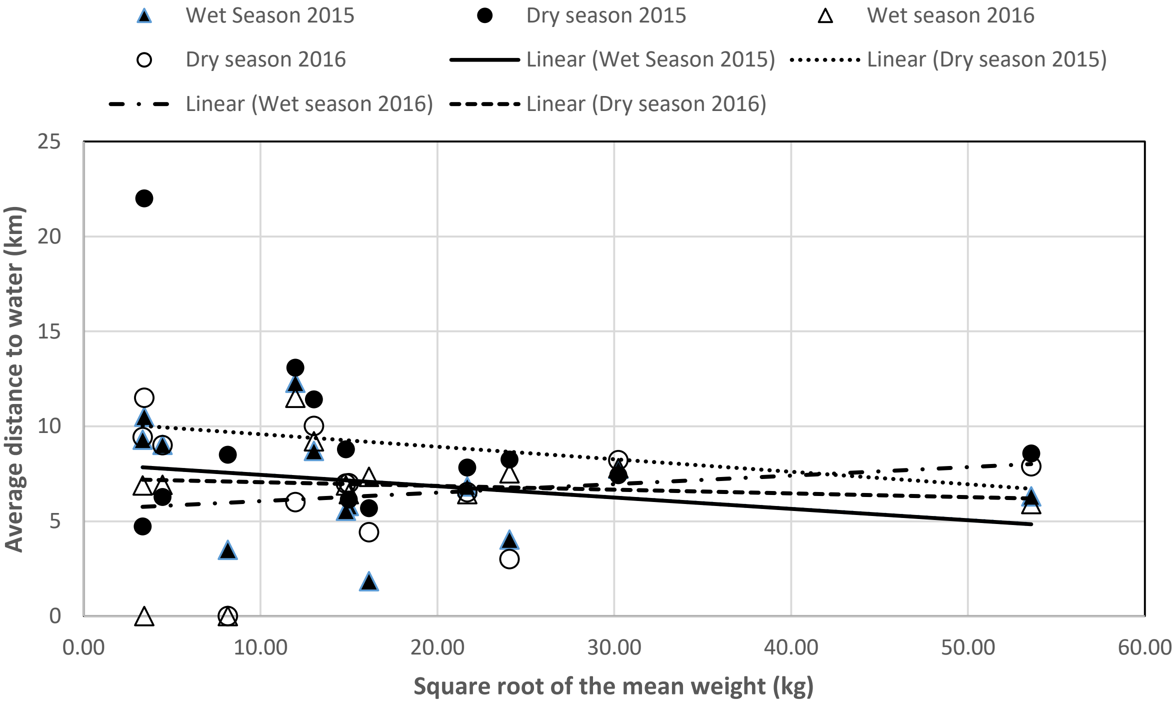

Figure 3.4. Correlation between mean weight and average distance from the closest water point for the wet and dry season of 2015 and 2016

Results showed that annual variations were close to being significantly different (p-value=0.079), species are statistical significantly different in the average distance at which they are found relative to the water hole (p-value=0.035), seasonal variations do not show statistically significant differences, neither was there any interaction significant difference between species and seasons (Table 3.2). Klipspringer and red hartebeest where consistently found furthest from waterholes as compared to the other ungulates, whereas the warthog was found to be the closest to the waterholes (Table 3.2).

Table 3.2. Post hoc analysis of average distance to the water point across different animal species using Duncan’s multiple range test at 5 % significant level. Numbers sharing the same letter are not statistically significantly different at 5%.

Species	**Homogeneous subsets**			
Warthog	3.00^{a}			
Roan	4.80^{ab}	4.80^{b}		
Eland	5.70^{abc}	5.70^{bc}	5.70^{c}	
Oryx	6.32^{abc}	6.32^{bc}	6.32^{c}	
Buffalo	6.88^{abcd}	6.88^{bc}	6.88^{cd}	6.88^{d}
Sable	7.04^{abcd}	7.04^{bc}	7.04^{cd}	7.04^{d}
Giraffe	7.18^{abcd}	7.18^{bc}	7.18^{cd}	7.18^{d}
Steenbok	-	7.58^{bc}	7.58^{cd}	7.58^{d}
Duiker	-	7.80^{bc}	7.80^{cd}	7.80^{d}
Kudu	-	-	9.82^{cd}	9.82^{d}
Red Hartebeest	-	-		10.72^{d}
Klipspringer	-	-		11.00^{d}
Sig	.114	.258	.122	.122

3.5 Discussion

Detection probability of ungulates in WNP decreased with increasing distance, though cluster size and abundance varied with increasing distance in the four vegetation as noted by Schroeder *et al*. (2014). The underestimation of abundance and densities of ungulates that might avoid roads and human disturbances was recognized. Hence, the accuracy of our results is based on the assumption that species distributions and densities were not different along roads than farther from roads (Schroeder *et al*. 2014). Probability of detecting animals consistently decreased as the distance from the transect increased as expected in the distance sampling theory. This suggests that ungulates did not avoid roads in the current study most probably due to the low level of disturbances associated with the roads in the park.

Distribution of ungulates is important in shaping vegetation structure and quality of ecosystem function and this can be influenced by the availability of water (Ogutu *et al*. 2010). Surface water is said to be one of the constraining resources for herbivore populations in semi-arid regions (Mwakiwa *et al*. 2012), thus it is important to understand how water points are used by different wildlife species in relation to their feeding guilds and body size (Rispel *et al*. 2016). Some species, such as warthogs are well known for being close to the vicinity of water points, whereas others, like steenbok and grey duiker even though small-bodied and also water dependent may venture at far off from the closest water points.

Anderson *et al*. (2016) suggested that ungulates respond to landscape heterogeneity according to the spatial and temporal distribution of resources and that variation among mammalian herbivores is created by the foraging constraints which arise due to herbivore body size. In WNP small bodied animals, such as the steenbok, were distributed evenly over the park irrespective of the season and this could mainly be because they are territorial and where not necessarily in the vicinity of the water points during the study as expected, whereas the intermediate body sized animals, such as the sable, and kudu were mostly distributed further away from the water points. This could be because water necessities generally scale with body size as shown by (du Toit 2002; Brown 2006).

Buffalo, as expected, appeared to be evenly distributed throughout the landscape, suggesting that they were not affected by the distance from or to the water points during both wet and dry season as noted by (Valeix *et al*. 2007; Loarie *et al*. 2009). Buffalo are by nature gregarious species, and are predominantly grazers that occur mostly in woodland to woodland savannah, (Macandza *et al*. 2012; Harris 2014; Fynn *et al*. 2014). They are able to fend off predators because of their large body size and large groups (Sinclair *et al*. 2003), which enables them to forage in wooded vegetation with relatively low visibility and high predation risk. They generally avoid heavily grazed regions of short grassland (Bhola *et al*. 2012; Traill & Bigalke 2007) which was evident in this study. In WNP, Buffalo avoided the Rocky community vegetation (*Peltophorum africanum*) which is rather an open vegetation with little to no cover and the tree shrub vegetation (*Terminalia sericea-Melhania acuminate*) and preferred the thorn bush vegetation (*Terminalia sericea-Blepharis integrifolia*) and the tree shrub (*Terminalia sericea-Thesium megalocarpum*).

Based on prior studies, the roan antelope is known to be found further away from the water points (Smit *et al*. 2006), even if it said to be very water dependent, it is also known to be very shy and avoids open areas making them rare to see around water points. This doesn’t seem to be the case in WNP where during both dry and wet season of 2015-2016, roans where regularly found close to the vicinity of the waterholes. Roan antelope are predominantly grazers and gregarious species associating in small herds. Roan are confined to lightly wooded savanna with extensive open areas of medium to tall grasses (Terungwa *et al*. 2009), where water is available. In Kruger National Park (Joubert 1976), noted that roan avoided woodland. They tolerate low bush growth in the grassland and avoid areas of short grass with open stands of medium to tall grasses being an essential habitat requirement (Skinner 2005). In WNP, roan avoided the tree shrub (*Terminalia sericea-Melhania acuminate)* and rocky community (*Peltophorum africanum*), whilst preferring the thorn bush vegetation (*Terminalia sericea-Blepharis integrifolia)* and the tree shrub savanna (*Terminialia sericea-Therium megalocarpum*).

Red hartebeest are regarded as water dependent but they may move a reasonable distance from water points to forage (Smit *et al*. 2009). Red hartebeest are predominantly grazers and gregarious species meaning that they are usually found in small herds. They are associated predominantly with open grassland of various types including floodplains grassland, semi-desert bush savanna and to a less extent in open woodland. They avoid the more closed types of woodland, except when in transit (Skinner 2005). They are predominantly selective grazers that will make use of browse under limited resource conditions (Venter *et al*. 2017). In this study, the red hartebeest preferred the thorn bush (*Terminalia sericea-Blepharis integrifolia*) whilst avoiding both the rocky community vegetation (*Peltophorum africanum*) and the tree shrub savanna (*Terminalia sericea-Melhania acuminate).*

Mobility is another factor that could have influenced the distributions of species around the water points, some species like kudu, buffalo and roan antelope are known to walk long distances from the water points (Smit *et al*. 2006) to feed. This could be explained by the wider food quality tolerance which allows large bodied species to use a higher diversity of habitat types. This could also explain why species of different bodied sizes showed differences in dispersal from the water holes, particularly the buffalo, (Bell 1971). This allows the large bodied species to use larger proportion of the landscape by using a higher diversity of habitats, including those of low resource quality for the smaller species.

Water availability constraints on herbivore distributions have been shown to vary between feeding guilds (Redfern 1995) and that browsers tend to occur further away from water than grazers (Western 1975). Our results do not fully support this premise as the red hartebeest, eland and buffalo (grazers) in our study were mostly found further away from the water holes, while other grazers like the roan antelope and sable were rather intermediate with the distance from the water holes. Smit *et al*. (2007), suggested that herbivores do in fact exhibit different distribution patterns around water holes. They found out that the grazer’s species associated more with artificial waterholes, whereas the browsers and mixed feeders were indifferent to the water holes, suggesting that they were not confined to the water points. Species most impacted by water availability are those which have the highest biomass density within the grazer community, for e.g. the buffalo, (Owen-Smith 1996). (Redfern 1995) found that impala herd densities decreased with increasing distance to the water hole, while the distributions for giraffe and kudu were characterized by a weaker relationship between assemblages and distance-to-water.

Kudu are predominantly browsers, meaning that they may graze on fresh grass but browse a greater variety of plants. They are gregarious and herds are usually small. They are savanna woodland species that avoid desert, forest or open grassland areas, except in transit (Skinner 2005). In the semi-desert areas like Namibia, they tend to be localised, only being found where there is sufficient woodland that provides them with protection and food. In WNP, they especially avoided the rocky community vegetation (*Peltophorum africanum*), and preferred the thorn bush (*Terminalia sericea-Blepharis integrifolia*) and the (*Terminalia sericea-Melhania acuminate).* As noted by (Pienaar 1974), kudu in arid savanna prefer woodland, open tree savanna, shrub savanna and partial grassland vegetation but avoid thickets.

Eland are predominantly grazers and are also gregarious species usually occurring in small herds but can also be observed in large aggregations (Skinner 2005). The eland, like the greater kudu is able to exploit a wide variety of habitats, ranging from relatively moist savanna regions to sub-desert and desert (Pienaar 1974). In WNP, the eland preferred the rocky community vegetation (*Peltophorum africanum*) in both the dry and wet season in 2016 whilst avoiding it in the wet season of 2015. In the wet season of 2015 the eland avoided the tree shrub savanna (*Terminialia sericea-Therium megalocarpum*) whilst preferring it in the wet season of 2016.

Oryx are gregarious species, occurring in herds of up to 300 (Skinner 2005) and are essentially a species of open, arid country. In Namibia they are specifically known to occur in open grassland, open savanna and in light open woodland. They can also be found in savanna woodland but are then more often in search of new feeding grounds in the more open areas within the savanna wooldlands. In WNP, preferred the tree shrub savanna (*Terminialia sericea-Therium megalocarpum*) and the tree shrub savanna (*Terminalia sericea-Melhania acuminate).* Sables are gregarious species that prefer savannah woodland. They prefer open woodland with adjacent valleys and grassland with medium to high stands of grass and avoid woodlands (Chirima *et al*. 2013). They are predominantly grazers but can also browse to a small extent, specifically towards the end of the dry season when the nutritional value of grasses is low (Skinner 2005).

Sables are known to be dependent on cover and the availability of water. Studies done in Kruger National Park have revealed the lower physiological water requirements of sable which allow it to occupy habitats away from more water-dependent species, like zebra (Cain *et al*. 2012). In WNP, sables strongly preferred the thorn bush (*Terminalia sericea- Blepharis integrifolia)* and avoided the tree shrub savanna (*Terminialia sericea-Therium megalocarpum)*. In the Matobo National Park in Zimbabwe the most important grass species in their diet were *Brachiaria nigropendata* and the *Eragrostis spp* during the dry season (Grobler 1981) and both these grass species are found in both the vegetation preferred by the Sable in WNP. In the Pilanesberg Game Reserve the main grass species in their diet in the dry season was *Chrysopogon serrulatus* (Owen-Smith 2013), which does not occur in the WNP.

To summarise, we looked at the wet and dry season distribution of herbivore species in relation to their distance from the water points and in four different vegetation types. The habitat use of species within WNP was associated with the presence of particular vegetation types as defined by the underlying geology of the park, the species body size and their distance from the water points. Nevertheless, the habitat use shown by the different species appeared compatible with expectations. We predicted all species densities to decrease with increasing distance from the water points and densities decrease with increasing distance from the water points more so for the buffalo, roan, sable, giraffe and oryx. The results provide empirical proof as to which species associate with which vegetation type and their association to the waterpoints on a spatial and temporal scale in the WNP.

Furthermore, the results indicate that ecological processes or habitat characteristics associated with the distribution of water points, act as strong drivers of herbivore distributions in semi-arid African savannas. This is evident as consistencies and differences between distribution patterns of herbivore feeding groups (grazers, browsers and mixed feeders) on different geological vegetation types. Hence, waterpoints especially artificial ones become features in the landscape that can change the distribution of large African herbivores, even in a landscape where natural water is accessible. Extricating which factors contribute most strongly to the multi-species animal distributions, habitat use and ungulate abundance in WNP has to be done by considering a much larger suite of predictor variables that may influence each species distribution, habitat use and abundance and consequently comparing values of those predictor variables with other protected areas across southern Africa is highly recommended.

3.6 Acknowledgements

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List of Appendices

Appendix 3.1. Estimates of number of animals per hectare, where DS is Density estimates of clusters, E (S) is the estimate of expected value of the cluster size, D is the estimate of the density of animals and N is the estimates of the number of animals in specified area.

Parameter	Point Estimate	Standard Error	Percent Coef. of Variation	95% Percent Confidence Interval	
DS	0.10263E-01	0.43763E-03	4.26	0.94398E-02	0.11158E-01
E(S)	2.1722	0.70954E-01	3.27	2.0373	2.3160
D	0.22293E-01	0.11975E-02	5.37	0.20066E-01	0.24767E-01
N	3745.0	201.16	5.37	3371.0	4161.0

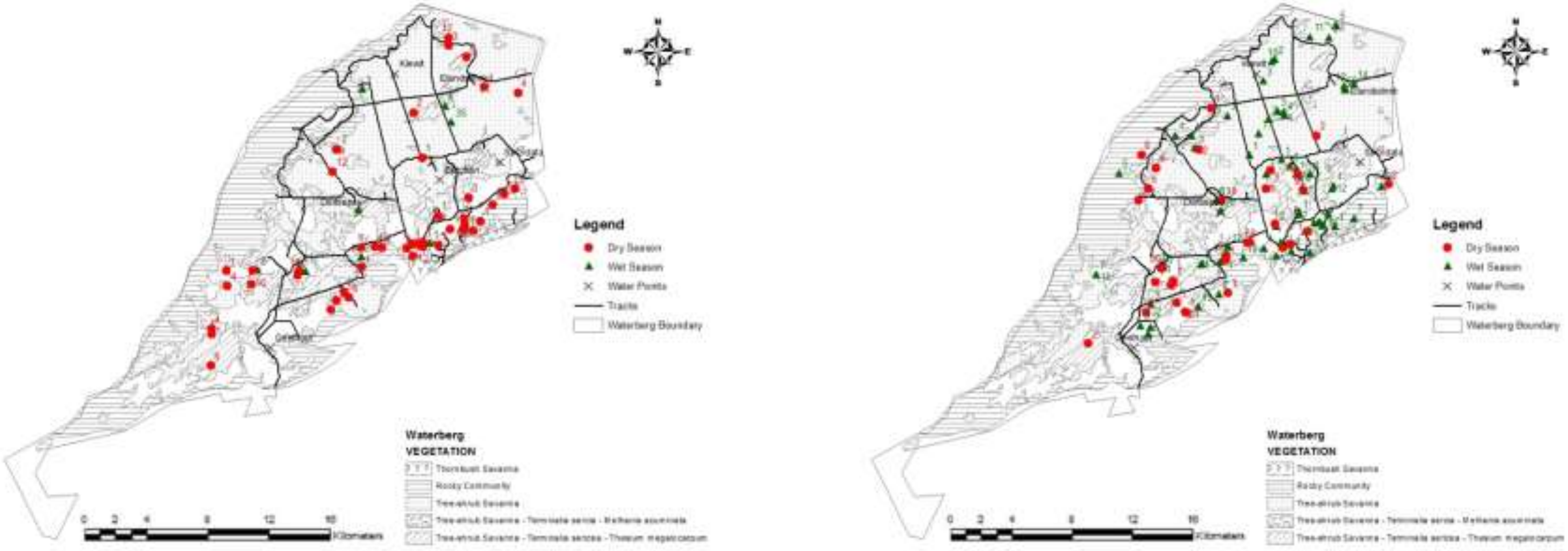
Appendix 3.2. Expected cluster size estimated based on regression of: log(s(i)) on g(x(i)), were (s(i)) is the cluster size of i-th observation and (s(i)) is the distance to the i-th observation.

Slope = -0.470000 Std error = 0.680951E-01

Intercept = 0.900656 Std error = 0.496068E-01

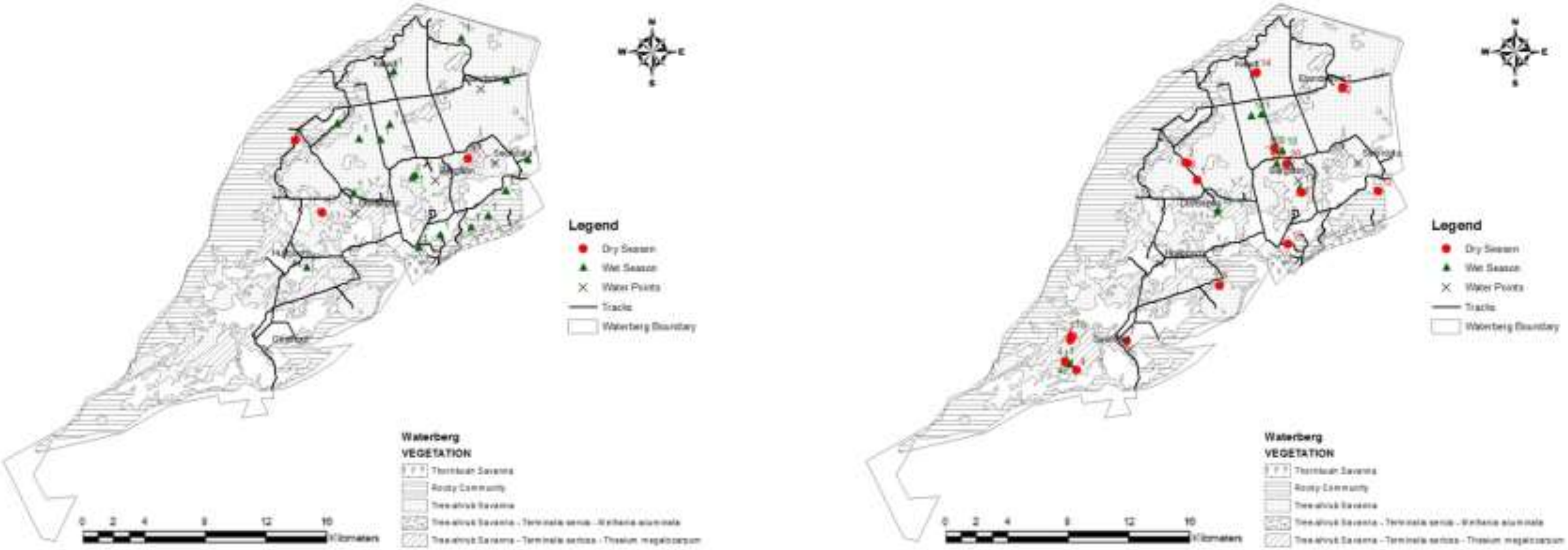
Correlation = -0.2281 Students-t = -6.90212

Df = 868 Pr(T < t) = 0.494227E-11

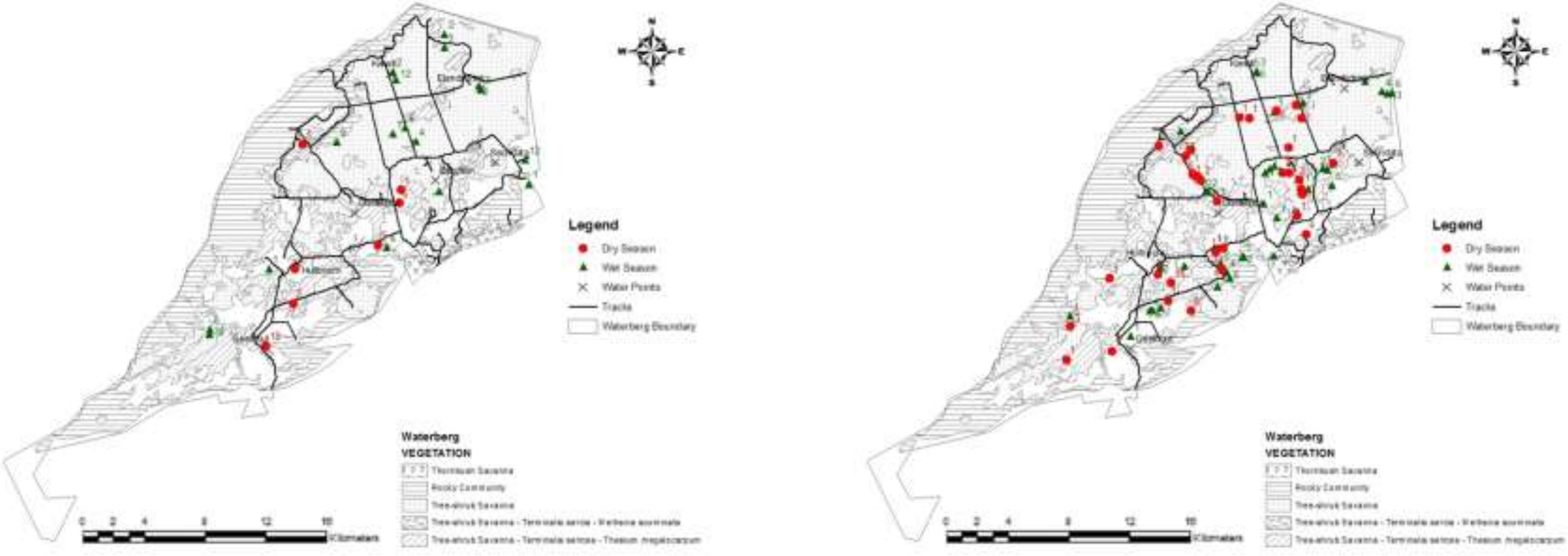


Appendix 3.3. Distribution of buffalo in relation to different vegetation types in dry (dots) and wet (triangles) seasons in Waterberg in 2015 (Left)-2016 (Right). The numbers near the symbols indicate the number of animals observed.

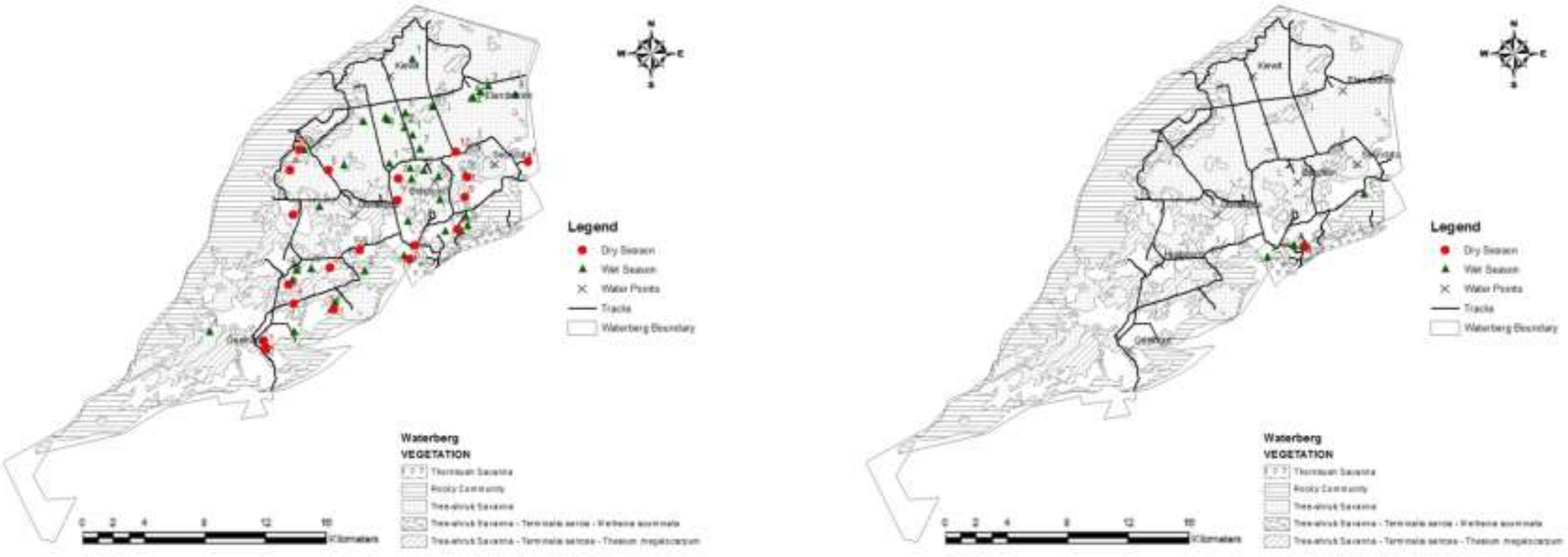
Appendix 3.4. Distribution of duiker in relation to different vegetation types in dry (dots) and wet (triangles) seasons in Waterberg in 2015 (Left)-2016 (Right). The numbers near the symbols indicate the number of animals observed.



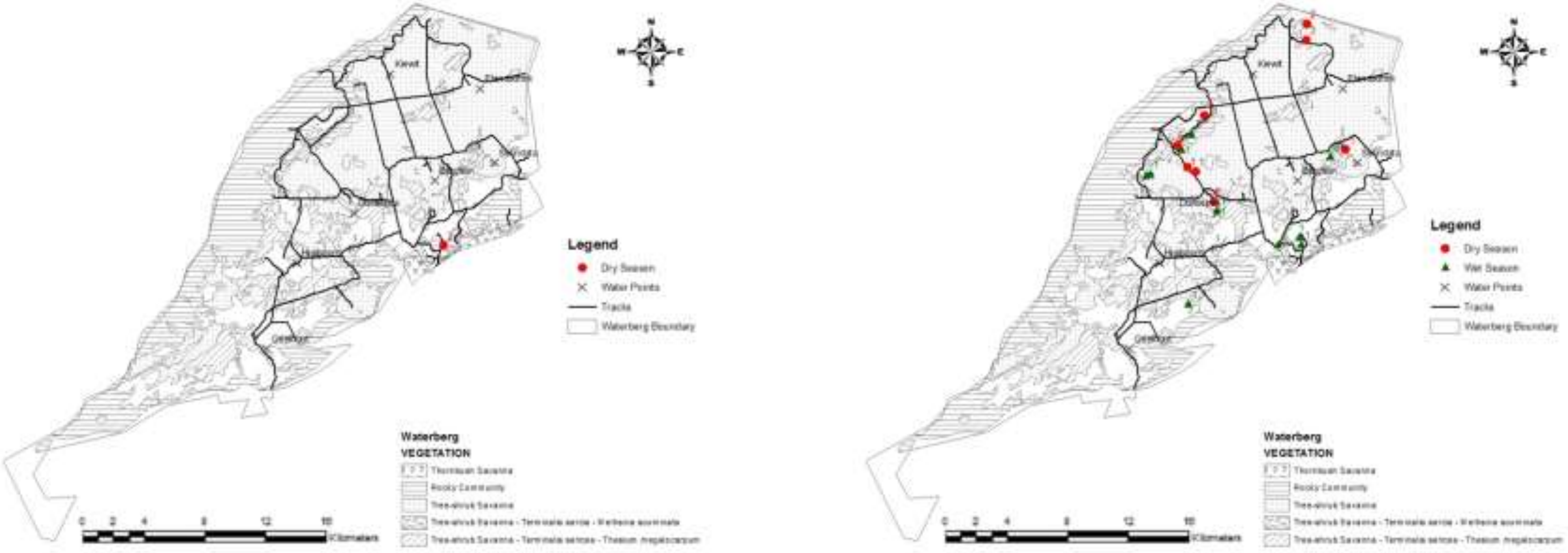
Appendix 3.5. Distribution of eland in relation to different vegetation types in dry (dots) and wet (triangles) seasons in Waterberg in 2015 (Left)-2016 (Right). The numbers near the symbols indicate the number of animals observed.



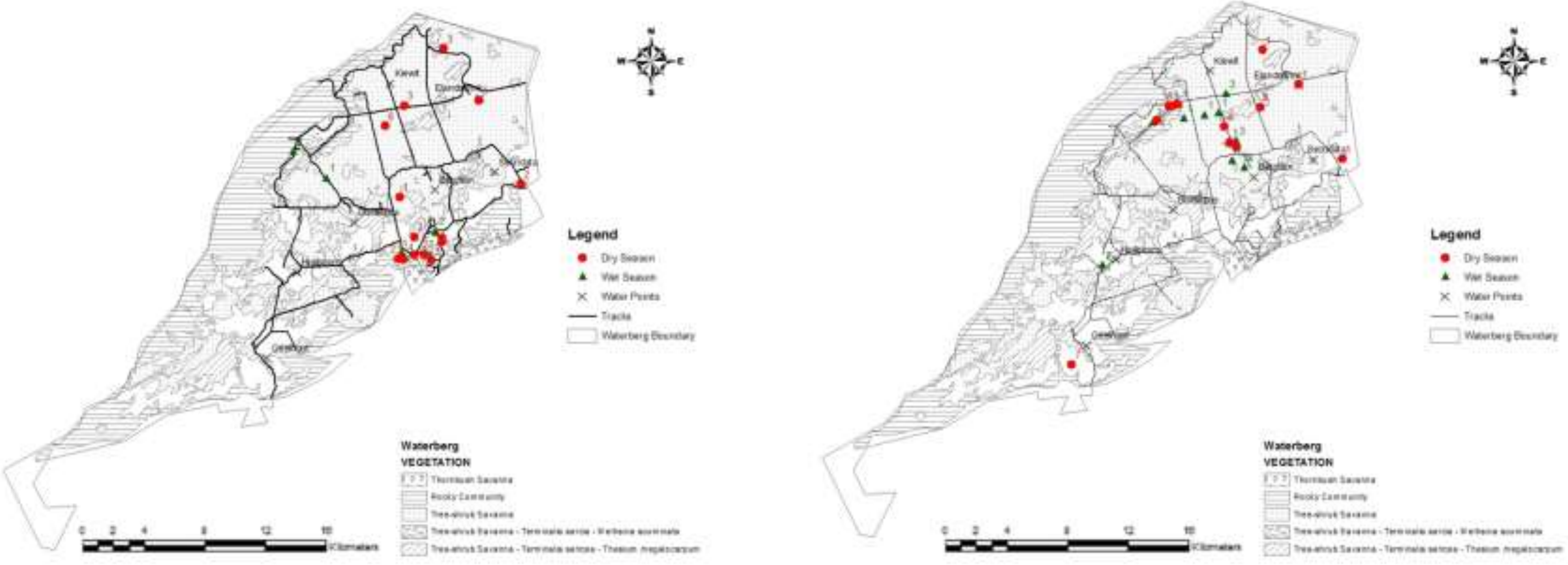
Appendix 3.6. Distribution of giraffe in relation to different vegetation types in dry (dots) and wet (triangles) seasons in Waterberg in 2015 (Left)-2016 (Right). The numbers near the symbols indicate the number of animals observed.



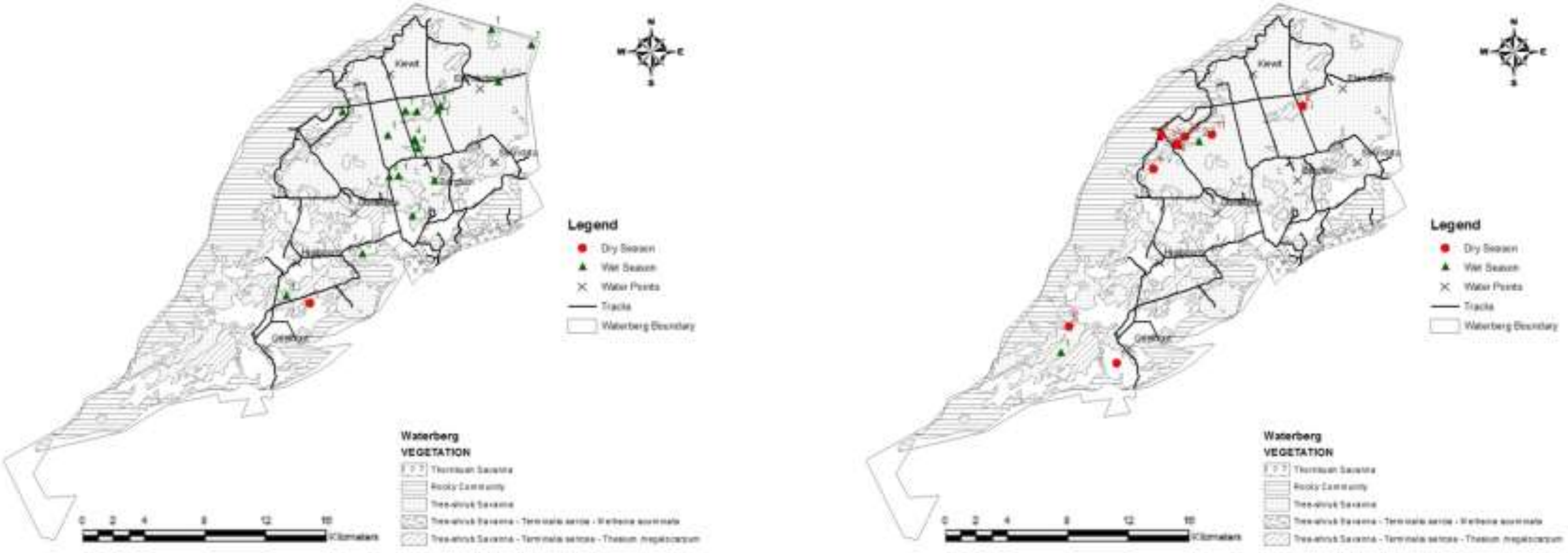
Appendix 3.7. Distribution of klipspringer in relation to different vegetation types in dry (dots) and wet (triangles) seasons in Waterberg in 2015 (Left)-2016 (Right). The numbers near the symbols indicate the number of animals observed.



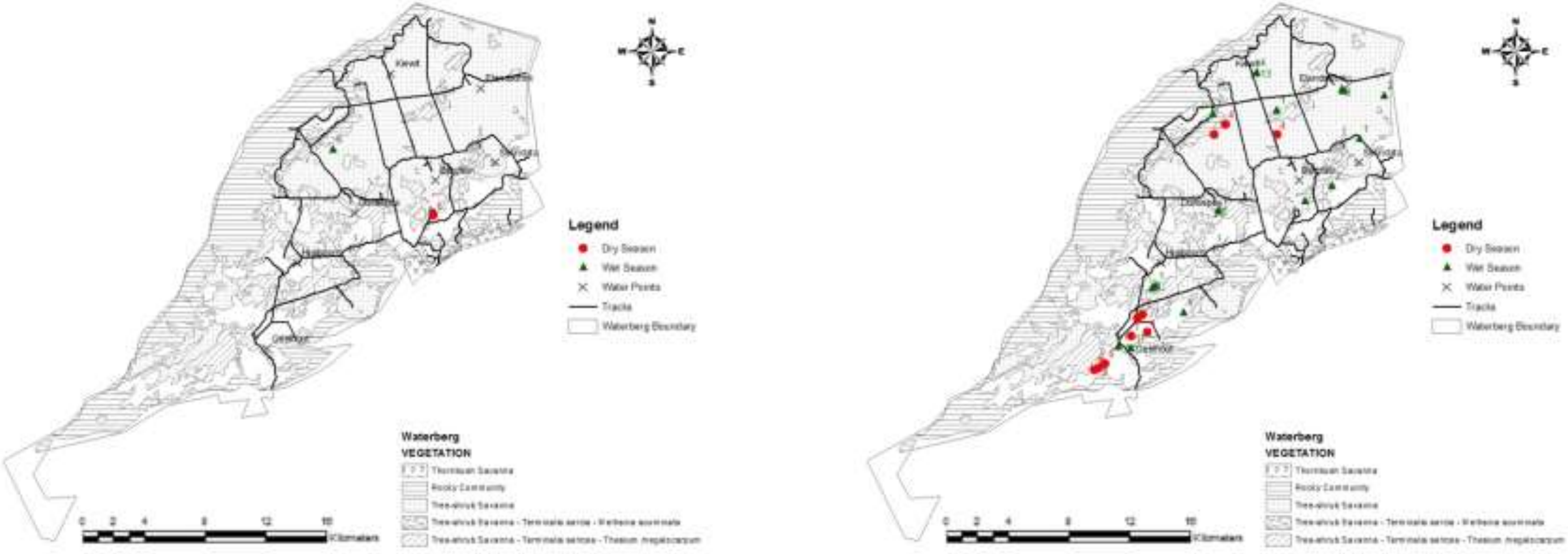
Appendix 3.8. Distribution of kudu in relation to different vegetation types in dry (dots) and wet (triangles) seasons in Waterberg in 2015 (Left)-2016 (Right). The numbers near the symbols indicate the number of animals observed.



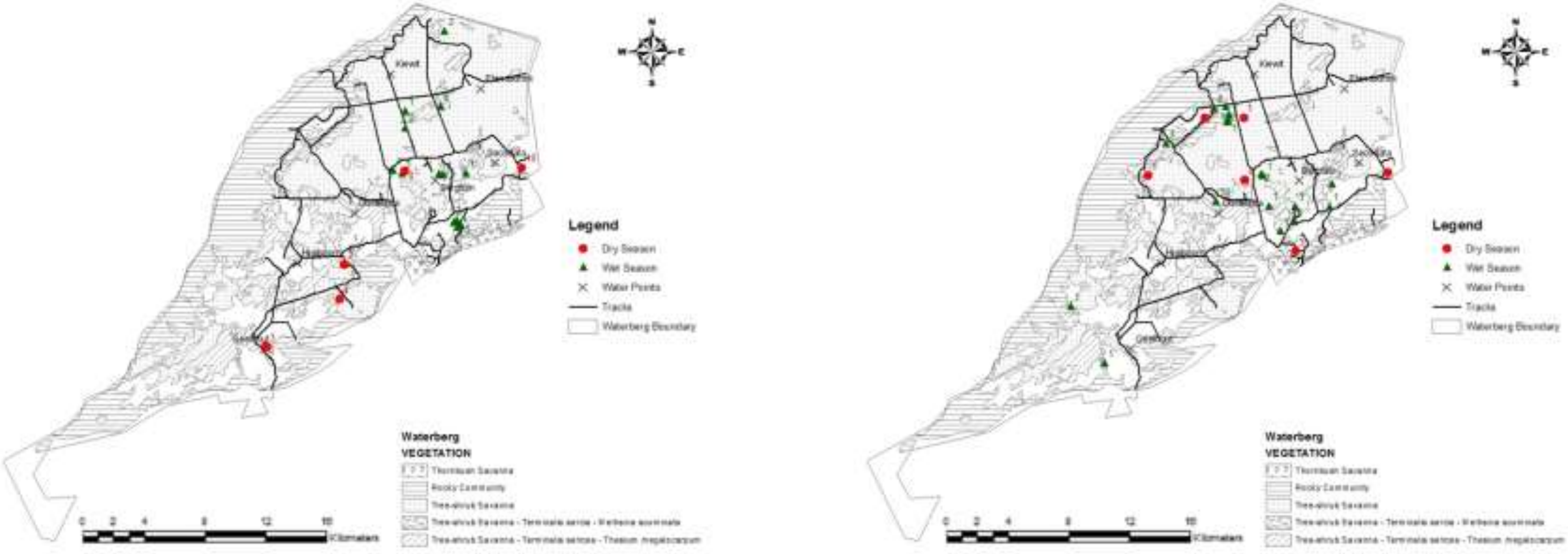
Appendix 3.9. Distribution of oryx in relation to different vegetation types in dry (dots) and wet (triangles) seasons in Waterberg in 2015 (Left)-2016 (Right). The numbers near the symbols indicate the number of animals observed.



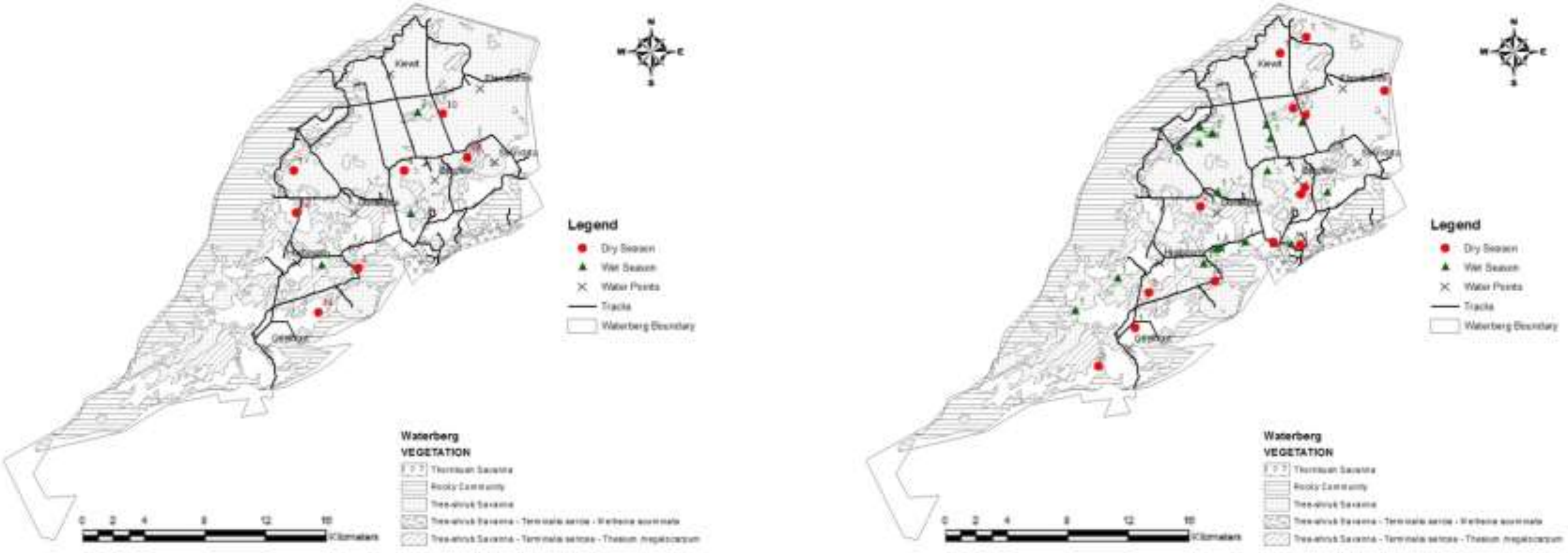
Appendix 3.10. Distribution of redhartebeest in relation to different vegetation types in dry (dots) and wet (triangles) seasons in Waterberg in 2015 (Left)-2016 (Right). The numbers near the symbols indicate the number of animals observed.



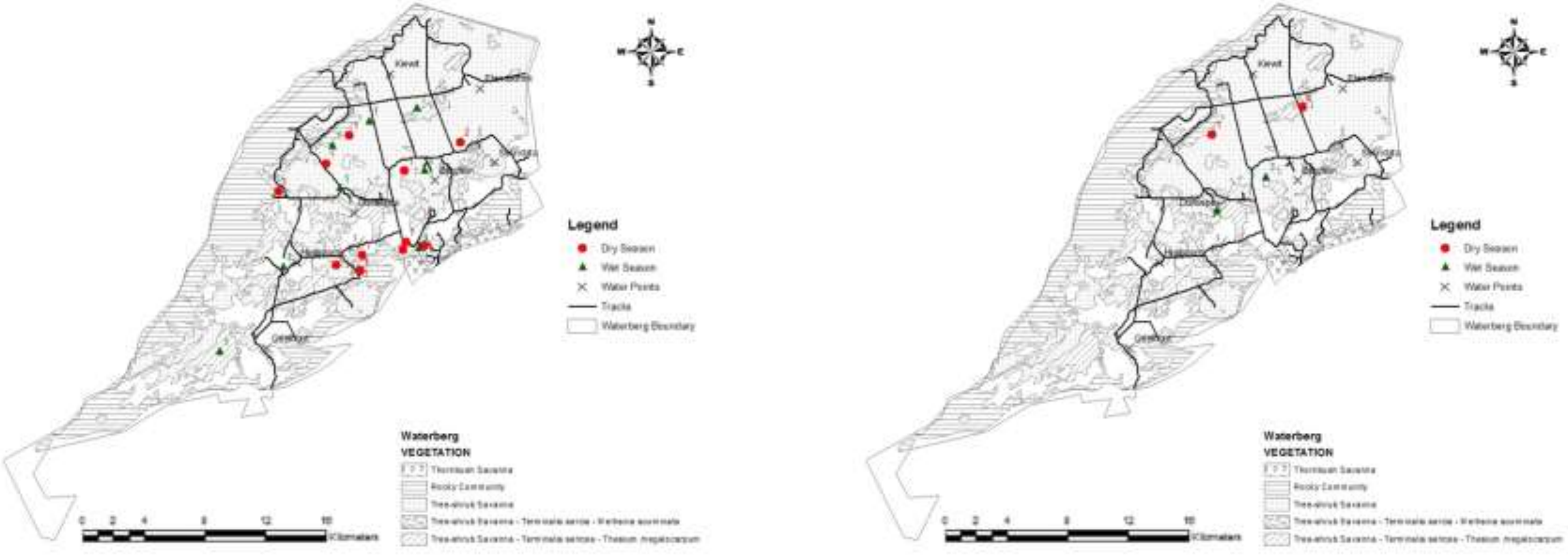
Appendix 3.11. Distribution of roan antelope in relation to different vegetation types in dry (dots) and wet (triangles) seasons in Waterberg in 2015 (Left)-2016 (Right). The numbers near the symbols indicate the number of animals observed.



Appendix 3.12. Distribution of sable in relation to different vegetation types in dry (dots) and wet (triangles) seasons in Waterberg in 2015 (Left)-2016 (Right). The numbers near the symbols indicate the number of animals observed.



Appendix 3.13. Distribution of steenbok in relation to different vegetation types in dry (dots) and wet (triangles) seasons in Waterberg in 2015 (Left)-2016 (Right). The numbers near the symbols indicate the number of animals observed.



Appendix 3.14. Distribution of warthog in relation to different vegetation types in dry (dots) and wet (triangles) seasons in Waterberg in 2015 (Left)-2016 (Right). The numbers near the symbols indicate the number of animals observed.

Appendix 3.15. Feeding preferences, social systems, average body mass, index of abundance and the number of observation of the species considered in this study.

Species	Scientific Name	Feeding types	Social system	Average body mass (kg)	Index of Abundance
Buffalo	*Syncerus caffer*	Grazer	Gregarious	471	100
Duiker	*Sylvicapra grimmia*	Grazer	Territorial	20	13
Eland	*Tragelaphus oryx*	Browser/Grazer	Gregarious	580	73
Giraffe	*Giraffa camelopardalis*	Browser	Gregarious	2870	58
Kudu	*Tragelaphus strepsiceros*	Browser	Matriarchal kinship	170	13
Oryx	*Oryx gazella*	Grazer	Gregarious	225	13
Red hartebeest	*Alcelaphus buselaphus caama*	Grazer	Gregarious	143	12
Roan	*Hippotragus equinus*	Grazer	Semi-gregarious	260	21
Sable	*Hippotragus niger*	Grazer	Territorial	220	15
Steenbok	*Raphicerus campestris*	Grazer	Territorial	11	12
Warthog	*Phacochoerus africanus*	Grazer/Browser	Matriarchal kinship	67	2
Klipspringer	*Oreotragus oreotragus*	Browser	Territorial	12	3

Appendex 3.16. Grass species found in the four main vegetation types in Waterberg N. P.

Grass species found in each vegetation type			
Terminalia sericea – Thersium megalocarpum	**Terminalia sericea - Melhania acuminata**	**Anthephora pubescus – Eragrostis superba**	**Peltophorum africanum**
Digitaria polevansii	*Digitaria polevansii*	-	-
Eragrostis pallens	-	*Eragrostis pallens*	-
Andropogon schirensis	-	-	-
Stipagrostis hirtigluma	*Stipagrostis hirtigluma*	-	-
Panicum kalaharense	*Panicum kalaharense*	-	-
Schizachyrium semiberbe	-	-	-
Aristida stipitata	*Aristida stipitata*	-	-
-	*Brachiaria nigropendata*	*Brachiaria nigropendata*	-
-		*Pogonarthria squarrosa*	-
-	*Rhynchelytrum repens*	*Rhynchelytrum repens*	*Rhynchelytrum repens*
Eragrostis stapfil	-	-	-
-	*Eragrostis jeffreysii*	-	-
-	-	*Anthephora pubescens*	-
-	-	*Eragrostis rigidior*	-
-	-	*Sporobolus fimbriatus*	*Sporobolus fimbriatus*
-	-	*Schmidtia pappophoroides*	-
-	-	*Eragrostis superba*	-
-	-	*Trichoneura grandiglumis*	-
-	-	*Eragrostis trichophora*	-
-	-	-	*Digitaria eriantha*
-	-	-	*Thynchelytrum bellespicatum*
-	-	-	*Diheteropogen filifolius*
-	-	-	*Loudetia ramosa*

CHAPTER 4: POPULATION STRUCTURE OF UNGULATES IN WATERBERG NATIONAL PARK, NAMIBIA (PAPER 3)

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4.1 Abstract

A study on the seasonal variation in population structure of seven (7) ungulate species, (African buffalo (*Syncerus caffer*), eland (*Tragelaphus oryx*), giraffe (*Giraffa camelopardalis*), oryx (*Oryx gazella),* sable (*Hippotragus niger*), roan antelope (*Hippotragus equinus*) and the greater kudu (*Tragelaphus strepsiceros*) was carried out using the field census approach during the wet (February-April) and dry (July-September) season, and a water hole census (September) at seven waterholes in the Waterberg National Park, Namibia. Male warthog, oryx and black rhino on average comprised about 40% of the population, whereas male sable, roan antelope, eland and buffalo comprised 30% of the population. Male kudu and male white rhino comprised 20% of the sex structure of the population, whereas male giraffe comprised more than 50% of population. Age structure was dominated by adults, with 60% of the total population in warthog, sable, eland and the white rhino, and 70% in kudu, roan, buffalo, giraffe and black rhino on average. Oryx had the highest number of adults, with only 10% of the population comprised of juveniles. Larger herds were observed during the wet season and smaller herds during the dry season. Animals were observed more abundantly in three of the vegetation types (*Terminalia sericea–Melhania acuminata* vegetation, *Terminalia sericea–Thesium megalocarpum, Terminalia sericea–Blepharis integrifolia*), with lower abundances in the rock-inhabiting *Peltophorum africanum* during both seasons.

Keywords: *herd size, sex and age structure, African ungulates, wildlife management*

4.2 Introduction

Africa has ungulate communities of unique diversity (Sinclair, 1983), in which the composition and population structure of both small and large herbivores varies considerably (du Toit, 1995). Ecological studies have shown that variations in abundance, activity or the use of sites by ungulates is linked to the seasons, scale of human activity, other species, or the availability of resources (Keuroghlian *et al*., 2004; Di Bitetti *et al*., 2008; Pérez-Cortez *et al*., 2012; Reyna-Hurtado *et al*., 2012; Pérez-Irineo *et al*., 2016). In large herbivores, habitat structure and population density are often reported as major determinants of group size variation within and between species (Marino *et al*., 2014). Hence, understanding the patterns of variation in abundance and community structure and the consequences for species diversity is a crucial point in ecology (Fritz *et al*., 2002; Hutchinson 1959; Gaillard *et al*., 1998).

Namibia is a semi-arid country, with several biomes (woodland, savanna, desert and Karoo) harbouring a vast variety of wildlife. The country has seven (7) national parks of which one is Waterberg National Park, which is the main source of rare and threatened species to all Namibia's national reserves and National parks. Unfortunately, in many species, populations are continuing to decrease within protected areas (Brashares *et al*., 2001; Newmark 2008; Tsindi *et al*., 2016; Gordon *et al*., 2004; Wilkie *et al*., 2011) often due to inconsistent rainfalls, temperature increases, recurrent droughts, disease outbreaks, poaching and trophy hunting (Milner-Gulland & Bennett, 2003; Winterbach, 1998; Ogutu *et al*., 2009). It is therefore crucial to understand population dynamics and the sensitivity of a population to these factors in informing conservation policy decisions and recovery strategies (Tsindi *et al*., 2016; Butler *et al*., 2013).

Fritz *et al*. (2002) suggested that African herbivore abundance and community structure are primarily determined by rainfall (Owen-Smith, 1990; Mills *et al*., 1995; Mduma *et al*., 1999; Georgiadis *et al*., 2003; Mason & Ogutu, 2005) and the nutrient status of the soil, by their effects on the quantity and quality of the primary production (Kennedy *et al*., 2003). The irregular availability of water in Namibia's semi-arid savannas affects the distribution, quantity and quality of food for large herbivores and hence, influences age and sex structure of herbivores with different dietary requirements across wet and dry seasons (McNaughton & Georgiadis, 1986; Davidson *et al*., 2013; Mduma *et al*., 1999). Herbivores in African savanna environments, and particularly in Namibia, depend strongly on rainfall received during the wet season for vegetation growth and hence food production (Rutherford, 1980). Coe *et al*. (1976)

suggested a model describing the variation in biomass of the ungulate communities based on annual rainfall, a good predictor of primary production across the globe (Lieth, 1975; Lauenroth, 1979), and specifically in sub-Saharan Africa (Le Houérou & Hoste, 1977; Desmukh, 1984).

Wildlife populations are also determined by the relative rates of natality and immigration versus mortality and emigration, and reflect the interplay of numerous, often widely variable, environmental factors (Masen, 1990). The spatial distribution of organisms is often regarded as being driven by a need to maximize fitness (Jones *et al.*, 2006), thus animals are expected to aggregate within the most favourable vegetation/habitat patches (Bailey *et al.*, 1996; Cezilly & Benhamou, 1996). Therefore, seasonal changes in the characteristics of the vegetation may affect spatial distribution over time (Illius & O'Connor, 2000). Seasonal changes are caused mainly by direct weather effects on plant primary production, in conjunction with variable grazing pressure resulting from changes in population density (Crawley *et al.*, 2004).

Many studies are now focusing on how sex and age structure affect the dynamic of ungulate populations (Coulson *et al.*, 2001). Juveniles and older individuals within a population normally have lower survival rates than prime-aged individuals (Gaillard *et al.*, 2000; Holand *et al.*, 2002), and males frequently have lower survival rates than females (Clutton-Brock *et al.*, 1997; Holland *et al.*, 2002). According to Bianchet *et al.* (2003), large herbivores have strongly age-structured populations, and this is primarily because recruitment often decreases as population density increases in unexploited populations, where the proportion of older adults may increase with density. Since survival senescence is common in ungulates (Gaillard *et al.*, 2014; Bianchet *et al.*, 2003), ignoring density-dependent changes in age structure could lead to apparent density-dependence in adult survival. The density of a population is associated with variation in age- and sex-specific vital rates and population dynamics (Nicholson, 1933; Gaillard *et al.*, 1998; Gaillard *et al.*, 2000; Mysterud, 2002). Therefore, it is important to know whether apparent changes in adult survival at high density (Fowler, 1987) are due to density dependence in survival, or to changes in age structure. If age structure was mostly responsible for changes in adult survival, increasing density may lower overall adult survival in naturally regulated populations, but not in harvested populations such as those in Waterberg National Park (Langvatn & Loison, 1999).

Moreover, apparent trends in population numbers based on water point counts may be subject to counting variability between successive years. Field classification of sex and age classes also has limitations, particularly in that they do not provide information on adult mortality, which is necessary for interpreting age ratios (Masen, 1990). Hence, a combination of water hole and field surveys should facilitate more reliable assessment of population trends by providing complementary data on population size and structure.

The aim of the present study is to increase the understanding on how the population structure differs among species in the WNP, Namibia. We specifically set off to determine 1) the relationship between species herd sizes and the four major vegetation types in WNP. We also investigated the 2) age and sex structure of species in WNP, and 3) the association between the field and water point census of herd sizes during wet and dry season of all species in order to find the most suitable sampling method.

4.3 Methodology

4.3.1 Study area

The study was conducted in Waterberg National Park, which is situated in the Otjozonjupa region in northern Namibia, 280 km N of Windhoek and 68 km SE of Otjiwarongo (20°25'S, 17°13'E). The WNP is 49 km long from SW to NE, and 8-16 km wide. It is 40,500 ha in size, with 40,000 ha on the plateau and 500 ha in foothills (Kasiringua *et al.*, 2017). The plateau has an elevation of 1850 m above sea level and between 100 to 300 m above the surrounding plain. The periphery of the plateau forms almost vertical cliffs, up to 300m high. The top of the plateau is made up of aeolianite (lithified dunes) of the Etjo Formation, which is ca. 200 million years old. The sandstone is covered with Kalahari sand (W. Hegenberger, unpublished report) (Fig. 4.1).

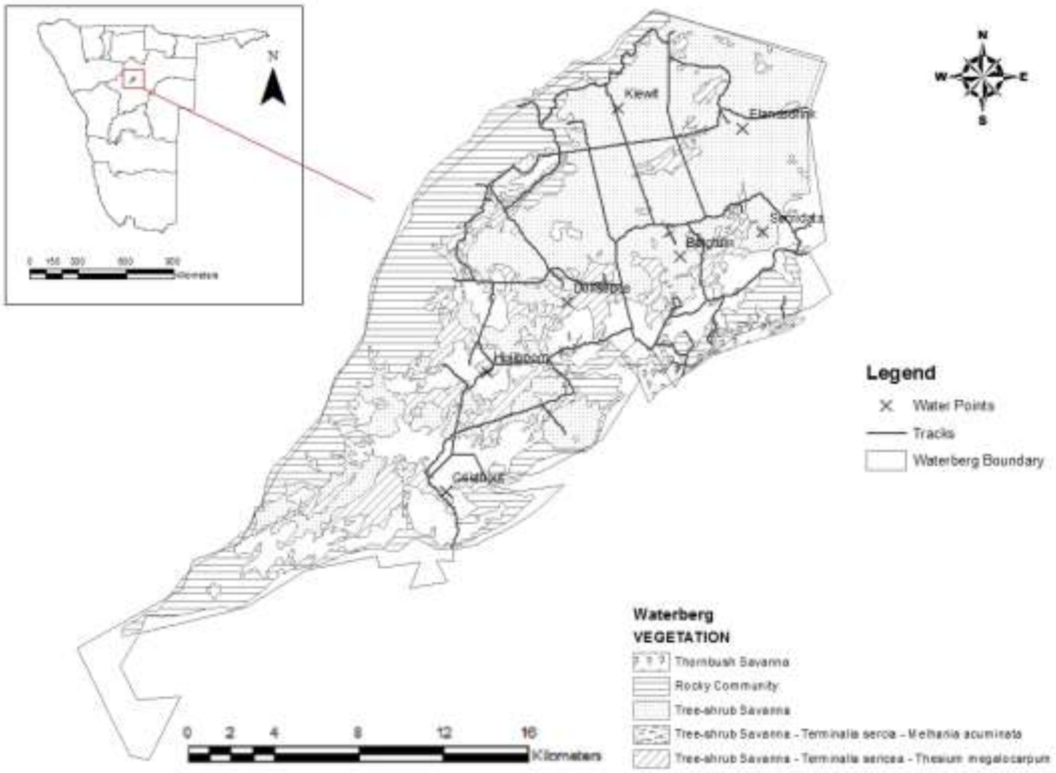

Figure 4.1. Location of WNP, the different vegetation types and the distribution of the seven (7) water holes in the park. Source: (Jankowitz, 1983).

There are no permanent water courses or pans. The water is pumped from the canal which runs across north central parts of the country from the Berg Aukas and Kombat mines where it is than diverted to the seven water points holes in WNP (Table 4.1), (Kasiringua *et al*., 2017).

Table 4.1. Location and elevation of the waterholes on the Waterberg National Park.

Water-Holes	Coordinates longit.	Coordinates latit.	Elevation
Bergtuin	20°22'45"S	17°21'14"E	1621m
Secridata	20°21'66"S	17°22'86"E	1598m
Elandsdrink	20°19'22"S	17°22'54"E	1621m
Kiewit	20°18'50"S	17°19'37"E	1647m
Duitsepos	20°23'57"S	17°18'16"E	1624m
Huilboom	20°25'47"S	17°15'69"E	1664m
Geelhout	20°28'56"S	17°14'64"E	1655m

The vegetation falls into the broad-leaf woodlands which are typical of the sandveld of eastern and north-eastern parts of Namibia (Mendelsohn *et al.*, 2009). Three main vegetation communities within this park have been recognized, with a fourth one occurring on rocky substrates: *Terminalia sericea–Melhania acuminata*, *Terminalia sericea–Blepharis integrifolia*, *Terminalia sericea–Thesium megalocarpum*, and the rock community *Peltophorum africanum* (Jankowitz, 1983). More than 90% of the rainfall occurs from October-March and has an average annual rainfall of 450.2 ±75.4 mm (Mendelsohn *et al.*, 2009) (Fig 4.2).

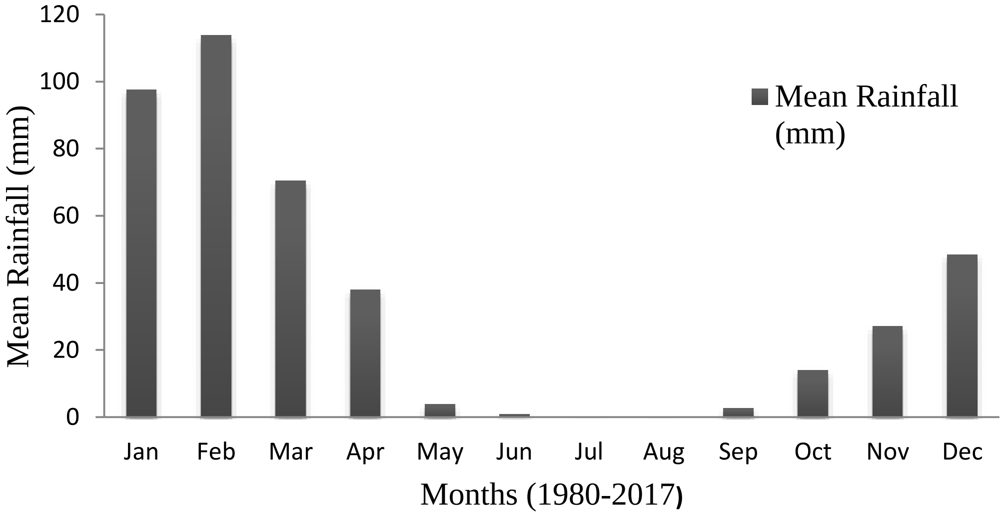

Figure 4.2. Rainfall in the Waterberg National Parik for the years 1980 to 2017. Source: (Sasscalweathernet.org/station_datasheet_we.php).

4.3.2 Data Collection

We studied only seven (African buffalo (*Syncerus caffer*), eland (*Tragelaphus oryx*), giraffe (*Giraffa camelopardalis*), oryx (*Oryx gazella)*, sable (*Hippotragus niger*), roan antelope (*Hippotragus equinus*) and the greater kudu (*Tragelaphus strepsiceros*) of the species using field census data (collected along road transects), simply because the census sample size of all the other species was too small. Census data from these seven species were then compared to the same species with data collected using the waterhole counts of herd sizes and numbers of herds. The main aim of the comparison was to determine the best sampling method between the two and to see if they would yield the same results. The waterhole census included other species like black rhino (*Diceros bicornis*), white rhino (*Ceratotherium simum*), and warthog (*Phacochoerus africanus*) which were only represented by figures based on water point counts. We specifically avoided presenting total number of white and black rhino in WPN due to the ongoing measures by the Namibian Ministry of Environment and Tourism to prevent rhino poaching in Namibia.

Field census

Data were collected using the distance sampling method during three months of Namibia's wet season (February to April) in both 2015 and 2016, while the data for the dry season were collected during June to August, of both years. A 4x4 truck was used to drive along the road transects, at a speed between 15-20km/hour. Sampling was started at exactly 06:00am on every sampling day, with the odometer set to 0 at the starting point. Observations where done from the vehicle by two to three observers aided by binoculars. A Global Positioning System (GPS) was then used to plot the coordinates of the observed animals, and distance was estimated between 0 and 100m for accuracy of identifying the sexes of the observed animals. All animal observations beyond 100m where not recorded (0m was recorded as the distance when the animal was observed was on the road). The total distance of travelled per day varied between 50 and 70km. We avoided recounting of the same animal by not returning along the same transects.

Water point census

Observations were conducted from specially constructed wooden shelter (hides) situated in a close proximity (ca. 50 m) to the seven water holes. Observations were carried out in the dry season (September), when the animals usually concentrate near water holes. The counts were organized around full moon nights, to achieve greater visibility of the game during the night. Observations were aided by binoculars. At each water point, there were 2-3 observers counting animals visiting the water points for 48 hours, i.e. from 10h00 a.m. to 10h00 a.m. of the last sampling day of the years 2008-2013. Each animals coming for drinking was timed, counted and identified to species level. Whenever possible, each individual was also sexed and aged, and identified individually (especially rhinos and giraffe) as to avoid double counting of some individuals which come more than once to the water point. Animals were counted separately in each group. Animals were visually identified to sex and age classes using combinations of sexually dimorphic physical characteristics, such as morphological configuration, age-specific differences in body size, shape and size of horns (Ogutu *et al*., 2008). Body size, presence, length and shape of horns and coat colour were used to identify juveniles. Ages were not assigned to adult animals (Sinclair, 1995; Ogutu *et al*., 2008).

4.3.3 Statistical Analyses

Seasonal data for herd size was subjected to non-parametric Mann-Whitney U test because it satisfied the assumptions associated with the test (Zar, 1999). Data for the number of individual species in a vegetation type was subjected to Kruskal-Wallis H-test using IBM SPSS package (v. 22). The Kruskal-Wallis test is rank based non parametric test which is used to determine any statistical differences between independent and continuous or ordinal dependent variables (Ostertagova *et al*. 2014).

4.4 Results

Buffalo was characterised by the largest herd size compared to all other species, with 153 herds and a total of number of 824 individuals, followed by the giraffe that had 128 herds and 118 individuals. The herd size of eland was lower (49) compared to that of the giraffe but the eland had a higher number of individuals (517 individuals in total) within these herds (Table 4.2). The Mann-Whitney U test on herd size in relation to seasonal variability in the WNP in 2015/2016 showed statistical differences (P=0.002) between the dry and wet seasons, with 242 and 283 herds respectively.

Table 4.2. Herd sizes of all ungulate species found in Waterberg National Park

Species	Average	SD	Variance	No of herds	No of individuals
Buffalo	5.71	8.70	4.48	153	824
Eland	8.92	17.33	35.38	49	517
Giraffe	3.01	3.39	0.08	123	118
Sable	3.32	4.25	0.43	33	104
Roan	3.47	3.03	0.09	49	167
Kudu	3.18	3.95	0.29	39	95
Oryx	2.21	1.99	0.02	38	84
Redhartebeest	6.92	6.80	0.01	13	90
Duiker	1.10	0.34	0.29	86	95
Steenbok	1.09	0.36	0.27	52	57
Klipspringer	2.13	0.83	0.83	8	17

The average herd sizes for individual species varied in between wet and dry seasons, with buffalo, eland, giraffe and kudu registering high averages in wet season (Table 4.3).

Table 4.3. Herd sizes of different species in relation to season of year 2015-2016 in Waterberg National Park.

Species	Season	Average of herd sizes	SD	Variance	No of Herds
Buffalo	Dry	5.49	9.26	7.10	78
	Wet	5.93	8.14	2.44	75
Eland	Dry	5.52	7.10	1.24	21
	Wet	11.46	21.93	54.77	28
Giraffe	Dry	2.93	3.25	0.05	57
	Wet	3.08	3.54	0.11	66
Sable	Dry	3.8	4.44	0.21	16
	Wet	2.88	4.16	0.83	17
Roan	Dry	3.85	3.41	0.10	20
	Wet	3.21	2.77	0.10	29
Kudu	Dry	2.63	2.24	0.08	19
	Wet	3.7	5.08	0.95	20
Oryx	Dry	2.85	2.51	0.06	13
	Wet	1.88	1.62	1.75	25

Eland had the highest average herd size, standard deviation and variation of 11.46, 21.93 and 54.77 respectively. A Kruskal Wallis H test showed that there was no statistically significant difference in number of individuals between different vegetation types. χ^2 (2) = 6.545, P=0.088. Ungulates were abundant in three of the four vegetation types (*Terminalia sericea–Melhania acuminata, Terminalia sericea–Thesium megalocarpum, Terminalia sericea–Blepharis integrifolia*), and less abundant in *Peltophorum africanum*, (Table 4.4). Multiple pairwise comparisons of species using the Steel-Dwass-Critchlow-Fligner procedure was used. Chi-square test for the animal species, averaged over the four vegetation types, showed significant differences, (Table 4.4).

Table 4.4. Herd sizes of different species in relation to the four main vegetation types in Waterberg National Park.

	Terminalia sericea–Melhania acuminata		***Peltophorum africanum***		***Terminalia sericea–Blepharis integrifolia***		***Terminalia sericea–Thesium megalocarpum***	
Species	No. Herds	No. Individuals	No. Herds	No. Individuals	No. Herds	No. Individuals	No. Herds	No. Individuals
Buffalo	44	294	29	190	32	148	40	192
Eland	25	224	3	33	17	212	8	48
Giraffe	51	51	13	13	22	22	32	32
Sable	12	29	4	6	8	35	8	34
Roan	18	63	5	16	10	32	15	56
Kudu	15	44	6	4	6	28	8	19
Oryx	19	42	0	0	9	18	10	24
Mean rank		17.17		6.83		12.75		13.25
X^2 (P-value = 0.088)								6.545

Results indicated a p value of 0.591 at 5% significance between variance of field and water hole were similar. A comparison of the two sampling methods (field and water hole) was done to distinguish the best sampling method using herd sizes and number of herds observed (Fig. 4.3a-g). All number of herds decreased with increasing herd sizes in all species, and larger numbers of herds were observed using the water hole counts as compared to the field counts (Fig. 4.3a-g).

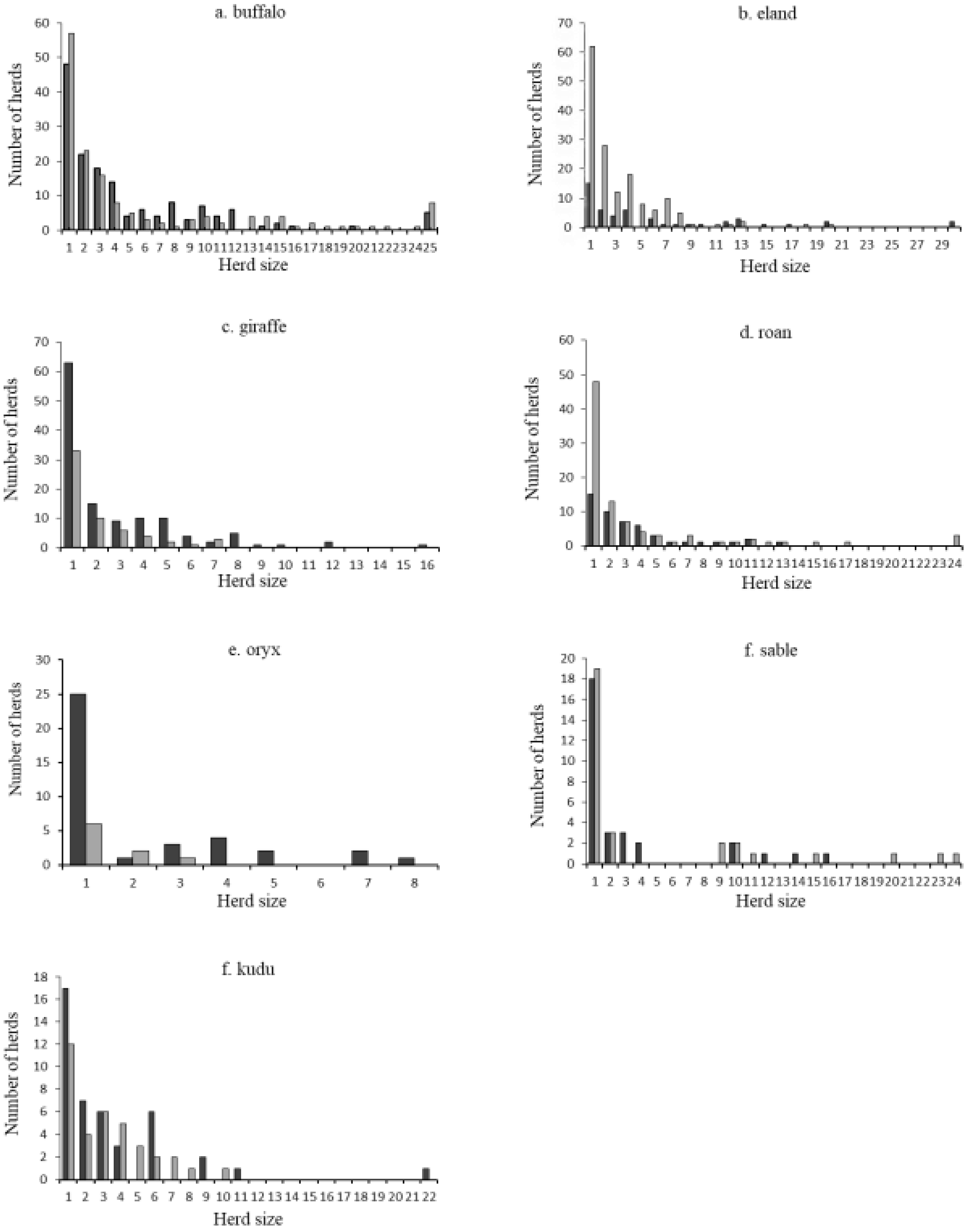

Figure 4.3. Herd size for ungulates in Waterberg Plateau Park (Field: black bar, Waterhole: grey bars).

The black rhino had larger number of herds in herd sizes 1-3, whereas in herd sizes 3-5 the white rhino had larger numbers of individuals than the white rhino (Fig. 4.4).

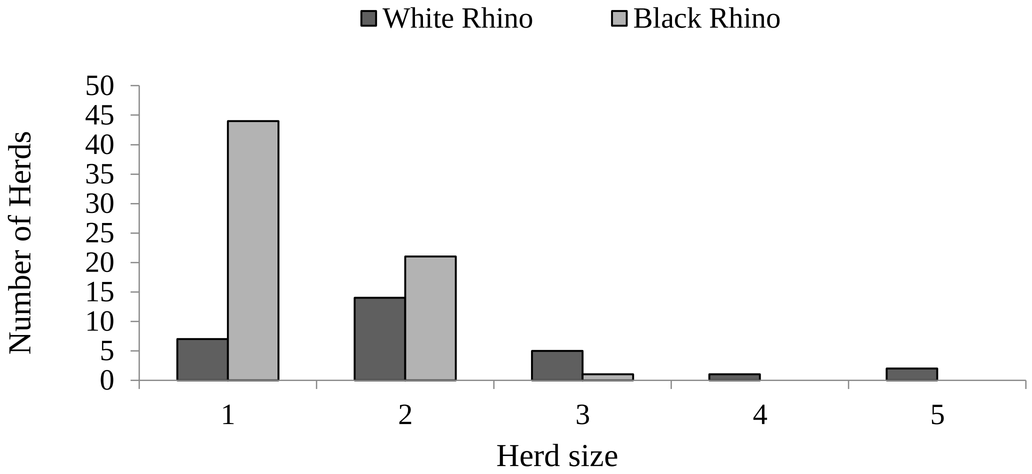

Figure 4.4. Herd size and number of herds of White and Black Rhino based on water point census only in Waterberg Plateau Park.

All species seem to have had larger numbers of herds in the herd sizes of 1-4 animals. Proportionally, there were fewer males species observed than females in WNP during the years 2008-2013 with the exception of the giraffe that showed a higher proportion of males than females (Fig. 4.5).

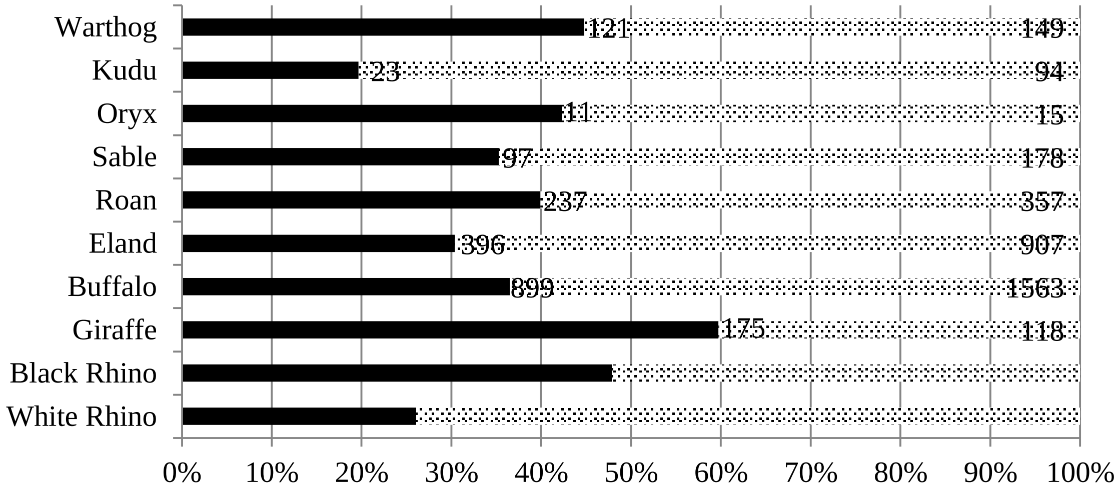

Figure 4.5. Year to year changes in the proportion of sex [Males: black bar, females: grey bars] in ungulates in the Waterberg Plateau Park in 2008-2013, based on water point census.

All species showed a higher proportion of adults as compared to the juveniles, least so the sable and eland (Fig. 4.6).

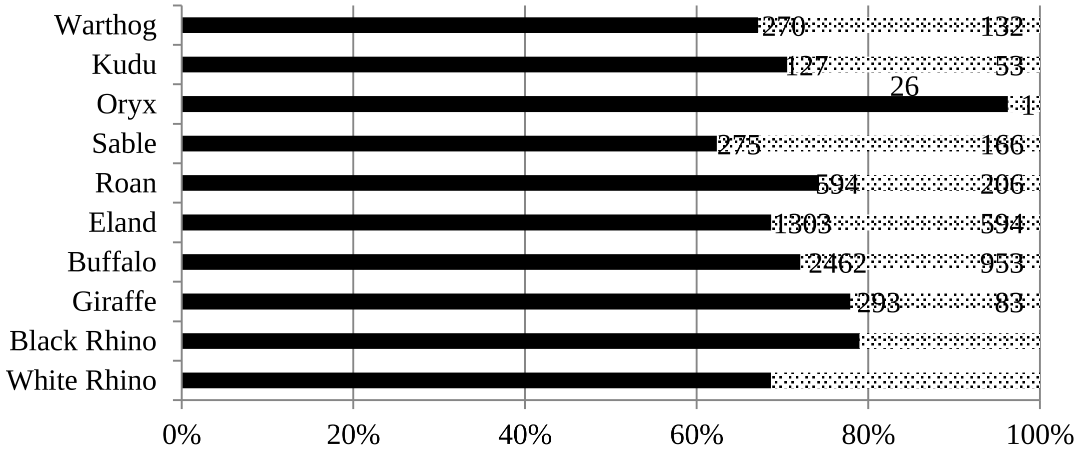

Figure 4.6. Year to year changes in age structure [Adults: black bar, Juveniles: grey bars] in ungulates in the Waterberg Plateau Park in 2008-2013, based on water point census.

4.5 Discussion

The fluctuation in rainfall, especially between the year 2013-2015 in WNP, may have played a fundamental role in the ungulate population structure and should be evaluated and accounted for before the effects of other factors (such as predation, disease, fire, etc.) can be considered. Other studies have confirmed that rainfall has a significant influence on the abundance of species, which could confirm population dynamics of species in a given area (Ogutu and Owen-Smith, 2003; 2006; Owen-Smith, *et al.*, 2005; Owen-Smith & Mills, 2006). All seven species showed an increase in number of herds and herd sizes in relation to the wet season of both years. Seasonal variation in rainfall effects were associated with seasonality in the number of recorded individuals, which contributed significantly to population fluctuation in all seven species.

The wet season census showed high herd sizes compared to the dry season herd sizes. This was primarily due to the better quality of fodder available during the wet season, because of the availability of growing grasses and bushes during the rainy season, which provides better fodder in the different vegetation as note by Megaze *et al*. (2018). Animals where more active during the wet season compared to the dry season, and this may be a result of the moderate temperature and cloudy weather conditions during the wet season as noted by Okello *et al.* (2015). The change in activity patterns of the different herd sizes during wet and dry seasons might be most likely due to changes in the availability of resources as observed by Ryan *et al.* (2006); Tshabalala *et al.* (2009); Ryan *et al.* (2012); Cornélis *et al.* (2014). Observations of smaller herd sizes in all the species during the dry season might reflect adaptations to a poor-quality environment, allowing the animals to better meet their energetic requirements (Megaze *et al*., 2018). In contrast, herd sizes of the buffalo, giraffe, sable antelope, roan antelope, kudu, oryx showed no major variation between wet and dry seasons (Melletti *et al*., 2007), but this was not the case for the eland which had an average herd size of 11.46 during the wet season and 5.52 during the dry season.

During both the wet and dry seasons, all the species formed larger aggregations in the *Terminalia sericea–Melhania acuminata* vegetation with scattered trees, than in the other vegetation types. This might be due to the abundance of food resources within the *Terminalia sericea–Melhania acuminata* vegetation, which can support large feeding herds or the fact that it covers an area twice the size of the other three vegetations. The *Peltophorum africanum* vegetation was least preferred by all the specie mainly because the area has a scarcity of grass and is a mostly rocky community.

Buffalo in this study area were mostly sighted in herds of four or less individuals but occasionally bigger herds of about 70 individuals were also observed, especially at the water points. Herds of solitary buffalo were most commonly observed. Herd sizes of the African buffalo in WNP varied by season. The wet season census obtained high buffalo herds and number of individuals within these herds compared with the dry season census. This was primarily due to the better quality of vegetation available during the wet season in the study area. The availability of growing grasses, bushes and the moderate temperature and cloudy weather conditions caused the animals to be more active than in the dry season. Higher numbers of juveniles were observed during this season, as buffalo mainly give birth during the wet season as noted in Vissher *et al*. (2004) and Turner *et al*. (2005). There was high proportion of females in the population. However, a low proportion of juveniles to adults (1:2.6) were observed during the present study. The male to female ratio of the buffaloes observed during the present study was 1:1.74 and agrees with the earlier observations in different parts of Africa (Prins, 1996; Vissher *et al*., 2004; Turner *et al*., 2005). In WNP, buffaloes were seen in smaller herds during the dry season and in larger herds in the wet season, similar to observations of savanna buffaloes as noted by Sinclair (1977) and Taylor (1989). The variation in buffalo herd size of during wet and dry seasons is a result of changes in the availability of resources as noted by Macandza *et al.* (2004) and Tshabalala *et al*. (2009). Melletti *et al*. (2007) and Korte (2008) reported that herd size of the forest buffalo showed no major variation between wet and dry seasons. African buffalo are said to congregate in large herds of 51-100 individuals as noted by (Eltringham *et al.*, 1973, ;Ryan *et al.*, 2006; Bennitt *et al.*, 2014), whilst Sinclair, 1977 reported that the average herd size in the Serengeti National Park was 350 individuals. In the present study area, the herd size of the buffalo was smaller. This may be justified in the context of patchiness and quantity of food resources in the different habitats. The pattern of herd size in the different habitat types of the study area was different and a scattered distribution of buffaloes was observed in the park.

The distribution of sable antelope within WNP was associated with the presence of particular land types, defined by vegetation features. Sable herds were more widely prevalent in the *Terminalia sericea–Blepharis integrifolia* vegetation**,** and less so in the *Peltophorum africanum* vegetation. Sable had more numbers of individuals in the *Terminalia sericea–Blepharis integrifolia* and *Terminalia sericea–Thesium megalocarpum* vegetation, although the latter generates more fertile soils and therefore more nutrient rich grasses. This pattern was also noted by Smit (2011). Highest sable average herd size occurred in the dry season.

Furthermore, sable herds were patchily distributed within landscape types and their presence seem to have been negatively dependent on the local abundance of two major grazers in the park (buffalo, roan). Roan and sable showed similar habitat preferences, with roan antelope concentrated especially in the *Terminalia sericea–Melhania acuminata* vegetation where sable herds were also recorded. The strongest negative effect on sable presence came from buffalo, which are grazers and widely distributed across the four habitats. Sable herds were unlikely to be present in the places where buffalo were concentrated at high density, whatever the habitat type. According to Cain *et al*. (2012), sable herds may inhabit areas further than 5 km from water and drink less frequently than daily, thereby avoiding the concentrations of other grazers that tend to develop near the water points. The proportion of adults to juveniles was 1:0.60 during the present study and male to female ratio of the sable observed during the present study was 1:1.84.

Other studies revealed that sable avoid close proximity to buffalo herds at a finer scale (Macandza *et al.*, 2012). Hence competitive interactions did not explain the influence of these grazers, apart from the grass height favoured by both the sable and roan antelope. Joubert (1974) and Magome (1991) noted that the sable herds tend to be secluded from concentrations of other ungulates. This might impose more predation on the sable calves, which could influence the local occurrence of the sable herds. Hence, the restrictions on the distribution of sable herds because of avoiding completion may cause high predation risks for the sable and this is consistent with evidence implicating elevated predation as primarily responsible for the population declines shown by sable (Owen-Smith *et al*., 2012) and the roan (Harrington *et al*., 1999).

The roan antelope is the second largest African antelope, distributed throughout the continent in sub-Saharan savanna habitat. Many populations are isolated and occur in low densities, and are declining. By comparison, sable in WNP were mostly associated with the *Terminalia sericea–Melhania acuminata* vegetation, where they had the larger number of individuals within these herds and least so in the *Peltophorum africanum* vegetation. The vegetation preference of roan antelope appears to be influenced by topography, vegetation type, availability of water, and competitors as reported by Wilson *et al*. (1977) and Havemann, (2014). Heitkönig & Owen-Smith, (1998) noted that roan antelope are most abundant in moist or dystrophic savanna and favour areas with few competitors or carnivores (Tyowua *et al*., 2012; Havemann, 2014). Their need to avoid extrinsic pressures such as competition and predation may be facilitated by their ability to tolerate low-quality food that other ruminants do not tolerate (Heitkönig & Owen-Smith, 1998). Roan herds usually roam less than 2-5 km from water (Grant *et al*., 2002; Martin, 2003; Kimanzi, 2011). In WNP roan antelope typically occurred in small herds, each with a dominant bull. The proportion of adults to juveniles was 1:0.35 during the present study and male to female ratio of the roan observed during the present study was 1:1.51.

Eland herd sizes and number of individuals within these herds varied from solitary animals to herds of 60 individuals in WNP. The largest herds always contained calves and juveniles, while the smaller herds comprised mostly of adult animals only. Herds were largest in wet seasons and smallest in dry seasons. Association preference in eland varied seasonally. In the dry season, females associations was mostly the basis of most herds, while female with juveniles were the nucleus of large rainy season aggregations. Such seasonal changes in herd sizes may be associated with food requirements. The proportion of adults to juveniles was 1:0.46 during the present study and male to female ratio of the eland observed during the present study was 1:2.29. In the present study, eland where associated more with the *Terminalia sericea–Melhania acuminata* and the *Terminalia sericea–Blepharis integrifolia* vegetation where the total number of individuals recorded was 224 and 212 individuals respectively. Eland have been classified as intermediate feeders preferring browse (Kerr *et al.*, 1970; Jankowitz, 1982;

Buys, 1990), while in others studies eland were found to be predominantly grazers (Lamprey, 1963; Underwood, 1975; Nge'the & Box, 1976). Some investigators have suggested that elands are not social animals, and they interact little with herd mates except for mating and mother to infant interactions (Kiley-Worthington, 1978; Hillman, 1987).

Interactions between individuals and family structure in giraffe have been described as temporary (Leuthold, 1979; Dagg & Foster, 1982; Pellew, 1984; Pratt & Anderson, 1985; Le Pendu *et al*., 2000). Loose relationships are thought to reflect weak herd structure in giraffe. Giraffe in this study area were mostly sighted in herds of five or less individuals, whereas in Hoanib River (Namibia) study area they were found in herd sizes of three and less individuals, (Fennessy *et al*., 2003). Solitary giraffe were most commonly observed (Fig. 3c), as noted in other giraffe populations throughout Africa (Scheepers, 1992; Le Pendu *et al*., 2000; van der Jeugd & Prins, 2000; Fennessy *et al*., 2003). Giraffe in WNP showed a rather peculiar trend in herd sizes and number of individuals within these herds. For each of the four vegetation types the herd size and number of herds were the same. Giraffe associated more with the *Terminalia sericea–Melhania acuminata and Terminalia sericea–Thesium megalocarpum* vegetation but avoided to the *Peltophorum africanum* vegetation. The proportion of adults to juveniles was 1: 0.28 during the present study and male to female ratio of the giraffe observed during the present study was 1: 0.67. The skewed ratio of males to females observed in the sex structure of giraffes could be the cause of conspicuousness by the males which could have made them easier to observe than the females.

Oryx are arid region mammals able to live indefinitely without free water (Taylor, 1969). Typically, oryx obtains water in waterless regions from their food by selecting food items with high water content (Taylor, 1969). We found that observations at water points were unsatisfactory for oryx, because the animals frequently fled and would not return. Most herds came and departed from water points as individuals or irregular herd. Individuals which arrived in herds at the water points often departed alone or with individuals already present at the water points. We conclude that the herds at water points were fortuitous collections of individuals, thus not necessarily of the same herd. A low proportion of adults to juveniles were observed (1: 0.04), and this could be caused by the type of landscape and the vegetation available in WNP, considering the fact that oryx are classified as rather arid to semi-arid mammals. Another explanation could be predation on the calves by the leopard (*Panthera pardus*), since the habitats in WNP are mostly dense making it an ideal hunting ground for the leopard. Male to female sex ratio was 1: 0.36, during the present study.

A total of 23 male and 94 female kudu were observed based on water point census. The sex ratio of males to females in WNP was 1:4.09. This ratio expressed the number of females per one male (1:4.09). The adult sex ratio found in this study was similar to sex ratios found for other kudu populations (Owen-Smith, 1990, 1993; Perrin & Allen-Rowlandson, 1995). The skewed sex ratio towards females may be due to a higher mortality rate for male kudu with increasing age. According to Annighöfer & Schütz (2011), male mortality accelerates sharply with age especially after reaching full weight at 6 years of age, as compared to females (Estes, 1997; Owen-Smith 1990, 1993). The proportion of adults to juveniles was (1:0.42). Kudu in WNP move in and out of the park, and are the only ungulates in the park known to do so. This is merely because of the topography of the park, which is partially fenced on the one side and governed by the steep slopes of rocks on the other where the kudu can climb down and up the mountain at their convenience, unlike most other species. Hence, the data presented here could be biased when it comes to reflecting the true picture of herd sizes of kudu in the park.

4.6 Conclusion

Age and sex structure requires constant monitoring in order to perceive changes in the demography of a population over time. Absence of adequate survey data on wildlife population structure and distribution prevents timely management and conservation decisions that could ultimately save many of the wildlife as suggested by Fynn & Bonyongo (2011). In conclusion, firstly, the number of herds and herd sizes in the different vegeations of the 7 different species appears to vary considerably between the wet and dry season in WNP. The sable and roan populations in WNP face a major decline in numbers because of their tendency to avoid habitats that are inhibited by other grazers or competitors like the buffalo. Hence, we suggest that the sable or roan antelope be relocated out of the park in order to reduce competition pressure by the buffalo. Relocation of the oryx to a more suitable environment might also the best option considering that they are finding it difficult to adapt to the current environment. Secondly, the study found that the general trend for the proportion of sex structure was generally higher for females except for giraffe. The high proportion of females to males indicates a positive chance for population growth of these species. Lastly, the use of the field and water point counts yielded no major difference in sampling sizes of most of the species, except for the oryx, implying that both sampling methods were satisfactory and should continue to be used to complement one another. The present results will provide baseline ecological data, and motivation for conservation efforts focused on wildlife management strategies that will improve the conservation of these rare species in the WNP.

4.7 Acknowledgements

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CHAPTER 5: RAINFALL AS THE KEY INDIRECT DRIVER OF AFRICAN UNGULATES POPULATION DYNAMIC (A NAMIBIAN CASE STUDY) (PAPER 4)

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5.1 Abstract

Population dynamics is the composite result of survival rates, reproductive success and movements of the animals forming a given population. Critical questions in the study of ungulate population dynamics include the mechanisms responsible for variability in vital rates and the contributions of density-dependent and density-independent factors. While numerous studies attempt to tease apart the effects of these factors, an ideal way to understand them is studying them in situations where some of them can already be assumed to have minimal influence. One such example would be a water-supplemented area experiencing no or minimal predation, and where the movement of individuals is limited by natural barriers such as mountainous ridges. The current study was undertaken to determine long-term population trends (33 years) of ungulate species in the Waterberg National Park (WNP), Namibia, which meets these conditions, using aerial and waterhole counts, and to compare the population trends observed here with those documented in other regions of sub-Saharan Africa. Most importantly, we try to investigate how rainfall indirectly influences the multi-species population dynamics in this system. During the years 1980-2013, seventeen ungulates species were recorded. Among these, eight have shown an increase in numbers during the years 1984-2013, six other decreased, and populations of two other species remained stable. Roan and sable antelope, kudu and warthog were also fairly common (with 5-12% of all ungulates recorded). White rhino, black rhino, giraffe, and gemsbok were classified as uncommon (together 11.9%), whilst the remaining seven species were rare (together 1.9%). Population size in eland showed a weak positive relationship with the annual average rainfall between the years 1981 - 2013, whereas population sizes in kudu, sable, gemsbok and roan showed a weak negative relationship with the amount of rain. No relationship was detected in giraffe, buffalo and hartebeest populations.We conclude that, irrespective of water supplementation, ungulate densities are to a large extent controlled by rainfall but in this study, other factors might have played a role in the dynamics of the ungulate densities. The rainfall effect can be explained indirectly, as rainfall determines plant growth and therefore the availability of forage.

Keywords: *aerial survey, population densities, population trends, rare species, African savanna, breeding areas, monitoring*.

5.2 Introduction

Population dynamics is the composite result of survival rates, reproductive success and movements of the animals forming a given population (Owen-Smith *et al*. 2005). The most important questions in the study of population dynamics of ungulates include the mechanisms responsible for variability in vital rates and the contributions of density-dependent and density-independent factors (Gaillard, *et al*., 1998; Brown, 2011). It is therefore vital to understand the environmental factors that influences ungulate populations dynamics.

From the point of view of wildlife conservation, some of the most important studies are those documenting population-level changes over medium to long-term time spans. Such knowledge can be used for the development and implementation of nature conservation strategies and for effective wildlife management, concurrently mitigating human-wildlife problems (Ranson *et al*., 2012). An absolute population estimate is often not a purpose of such studies. Relative estimate of population abundance may be sufficient, as long as the data are collected in a consistent manner (Sutherland, 1998). More important, therefore, is the use of the same or similar method over a long period of time. In African savannas, a biome which occupies about half of the surface area of the Afrotropical Region, hoofed mammals (ungulates), beside termites, often represent the main component of the animal biomass, and play one of the most important roles in matter and energy fluxes.

Over the last few decades, many ungulate species declined in numbers and subsequently became threatened by extinction over larger areas the Afrotropical savanna (Craigie *et al*., 2002). For efficient conservation and rational utilization of such species, it is important to monitor their populations on a regular basis. Such monitoring studies are of utmost importance and relatively easy to conduct in small to medium conservation areas, especially where these represent key breeding grounds for the target species. Examples of such conservation areas in southern Africa are the Addo Elephant (N. P.), Mountain Zebra N. P., Pilansberg N. P., Sandveld Nature Reserve., Ndumo Game Reserve, and the Waterberg National Park (WNP) in Namibia. To date, however, long-term monitoring programs on the entire ungulate assemblages have been conducted only in a few larger areas in southern and East Africa: Ngorongoro Crater, Tanzania (Runyoro *et al*., 1995), Kruger N. P., South Africa (Mills *et al*., 1995, Ogutu & Owen-Smith 2003, 2005), Hwange N. P., Zimbabwe (Chamaille-Jammes *et al*., 2009), the Laikipia District, Kenya (Georgiadis *et al*., 2007), Hluhluwe-iMfolozi Park, South Africa (Grange *et al*., 2012), and Masai Mara National Reserve, Kenya (Bhola *et al*., 2012).

Ungulates in arid and semi-arid environments experience considerable seasonal, climatic and spatial variation in resources (Illius and O'Connor, 2000), which affects the production of plant material and hence, indirectly, the carrying capacity of the ecosystem (Coe, 1976). Hence, environmental variability have a vital effect on the population dynamics of ungulates in arid and semi-arid grazing and browsing systems (Illius and O'Connor, 2000). Spatial variation in grazing and browsing systems in semi-arid areas arise from variation in soil characteristics and topography, which causes variation in nutrient content and hydrology. In addition, spatial variation of habitat selection and accessibility of the different species during the wet and dry seasons can be regarded as having important influences on the dynamics of ungulate populations.

Rainfall, predation, disease, vegetation productivity, density-dependent forage competition and irregular climate have been shown to significantly affect vital rates of ungulates (Messier, 1994; Solberg *et al*., 1999; Patterson & Power, 2002; Garrott *et al*., 2003). While numerous studies attempt to tease apart the effects of these factors, an ideal way to understand them is studying them in situations where some of them can already be assumed to have minimal influence.

One such example would be an area experiencing no predation or minimal predation. The movement of individuals is often limited by human-imposed barriers, but occasionally also by natural barriers such as mountainous ridges. The impact of rainfall on ungulates is twofold – direct, via water availability, and indirect, through vegetation productivity. A water-supplemented environment ensures that any effect of rainfall is in fact indirect. Despite the availability of systems where at least one of these conditions are met, not many studies have looked at population dynamics of multispecies ungulate assemblages in a high ridge mountainous area with little to minimal disease or large predators, or at the way in which rainfall indirectly affects populations in a water- supplemented environment.

In this study we try and investigate how rainfall indirectly influences the multispecies population dynamics in a water supplemented, disease free environment with little to no predators – the Waterberg National Park in Namibia. Camera-trap based survey confirmed the occurrence in the WNP of the following large carnivores: the leopard (*Panthera pardus*), brown hyena (*Hyaena brunnea*), spotted hyena (*Crocuta crocuta*), caracal (*Felis caracal*) and cheetah (*Acinonyx jubatus*). However, none of them are particularly abundant (Stein et al., 2008). The African wild dog (*Lycaon pictus*) appears in WNP only occasionally. Among the species listed above, it is likely that only the leopards may affect population dynamics of some of ungulates in the WNP. Leopard density in WNP was estimated at 1 individual per 100 km^2 (Stein *et al*., 2011). This is rather low in comparison with 3.6 individuals per 100 km^2 in the neighboring farms (Stein *et al*., 2011), but higher than in Etosha National Park (Standler *et al*., 1997). Predators can alter their prey selection in response to shifts in the relative availability of alternative prey species (Mills, Biggs & Whyte, 1995). There is also a body-size effect – often, the larger body size of a herbivore species, the lower its vulnerability to predation (Sinclair *et al*., 2003; Ripple *et al*., 2005). However, in WNP, especially prone to become leopard prey seem to be large species such as the warthog, roan and sable (Chapter 4).

In an initial, descriptive step this study aimed: 1) to determine population trends of all ungulate species in the WNP over the last 33 years using aerial and waterhole counts and 2) to compare the population trends with those documented in other regions of sub-Saharan Africa. However, more importantly, the study aimed 3) to testing the relationships between rainfall trends and the population dynamics of particular ungulate species, knowing that, due to water supplementation, these effects are primarily indirect, due to forage availability.

5.3 Methodology

5.3.1 Study Area

The study was conducted in the Waterberg National Park (Figure 5.1). It is situated in the Otjozonjupa region in northern Namibia, 280 km North of Windhoek (20°25'S, 17°13'E). The Waterberg National Park is 49 km long from south west to north east, and 8-16 km wide. It is 40 500 ha in size, with 40 000 ha on the plateau and 500 ha in foothills (Kasiringua *et al*., 2017). The plateau has an elevation of 1850 m above sea level, and between 100 to 300 m above the surrounding plain. The periphery of the plateau forms almost vertical cliffs, up to 300m high. The top of the plateau is made up of aeolianite (lithified dunes) of the Etjo Formation, which is ca. 200 million years old. The sandstone is covered with Kalahari sand (Hegenberger, 1988). There are no permanent water courses or pans. The water is pumped from the canal which runs across north central parts of the country from the Berg Aukas and Kombat mines where it is then diverted to the seven waterholes in WNP (Figure 5.1).

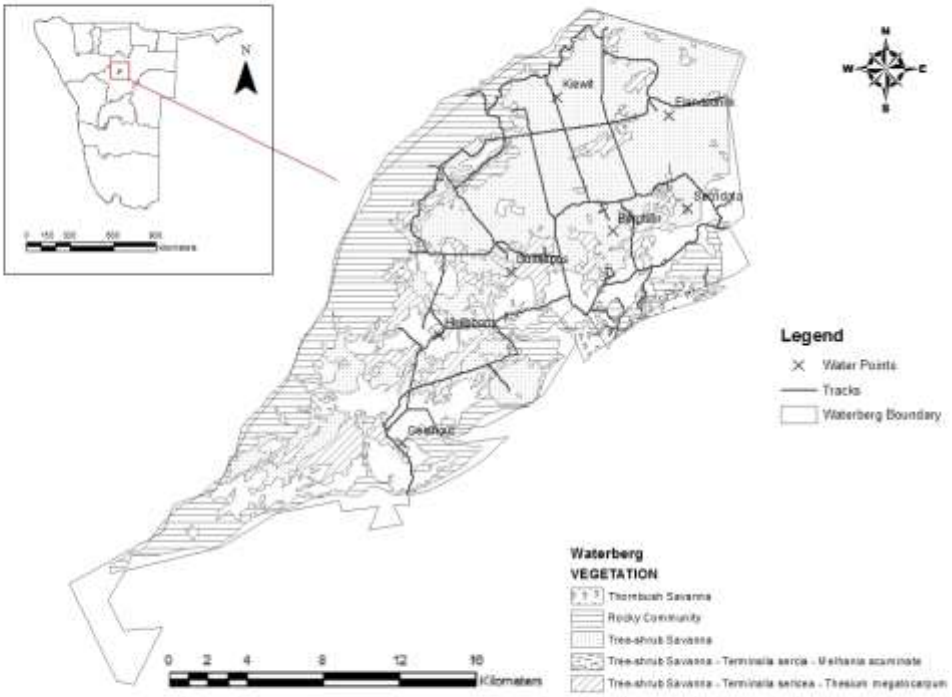

Figure 5.1. The main vegetation types on the Waterberg Plateau Park. Souce: (Jankowitz, 1983).

The vegetation falls into the broad-leaf woodlands which are typical of the sandveld of eastern and north-eastern parts of Namibia (Mendelsohn *et al*., 2009). Three main vegetation communities within this park have been recognized, with a fourth one occurring on rocky substrates: *Terminalia sericea-Melhania acuminata*, *Terminalia sericea-Blepharis integrifolia*, *Terminalia sericea-Thesium megalocarpum*, and the rock community *Peltophorum africanum* (Figure 5.1). Over 500 flowering plants and 140 lichen species are recorded from the Waterberg. Common trees include *Acacia ataxacantha, Burkea africana, Combretum collinum, C. psidioides, Dichrostachys cinerea, Grewia flavescens, G.retinervis, Lonchocarpus nelsii, Ochna pulchra, Peltophorum africanum, Terminalia sericea* and *Ziziphus mucronata*. Common grass species are *Andropogon schirensis, Brachiaria nigropedata, Digitaria seriata, Eragrostis jeffreysii, E. pallens, E rigidior* and *Panicum kalaharense* (Jankowitz & Venter, 1987; Mendelsohn *et al*., 2009).

The area has a mean annual temperature of just over 18°C. More than 90% of the rainfall occurs from October to March, and the average annual rainfall is 450.2 ±75.4 mm (Mendelsohn *et al.*, 2009). The rainfall between the years 1980-2013 varied considerably. The period 2001-2013 had the highest rainfall of the 33 years considered here, especially during the early months (January-March) of the year. In 1980-2000 there seemingly was more rain later in the year (September – December) as compared to 2001-2014. The years 2000 and 2013 were both drought years with no rain from January to December (Figure 5.2).

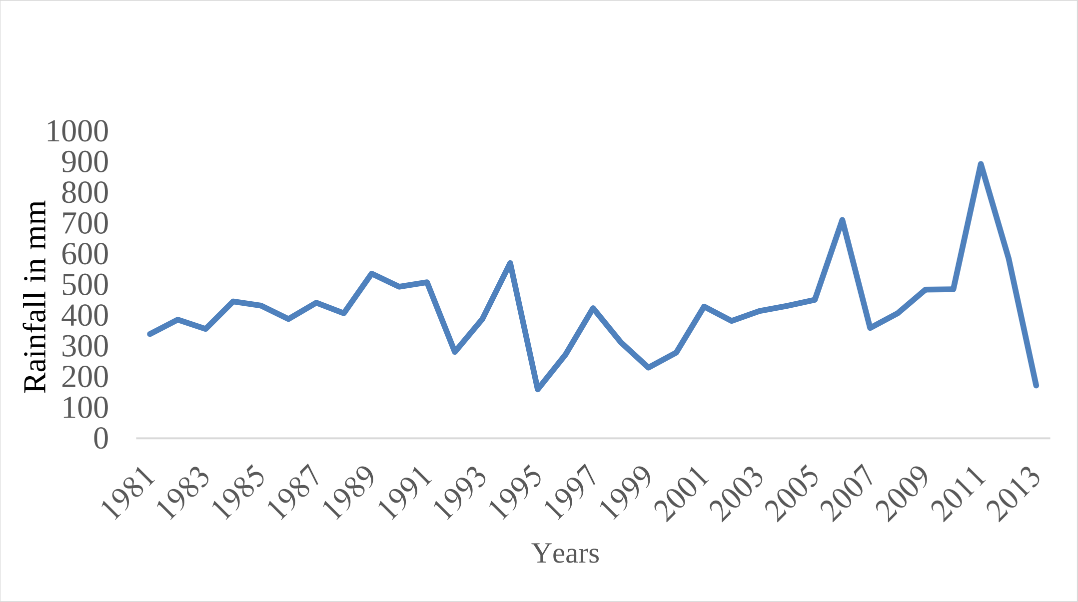

Figure 5.2. Rainfall in Waterberg National Park. Year to year changes in rainfall during the years 1981-2013. Souce: (Sasscalweathernet.org/station_datasheet_we.php).

Game management of these species in WNP is in accordance with the national Species Management Plan document (M.E.T, Namibia). The main aim of the park is breeding rare species of large mammals without negatively affecting biodiversity. Therefore, the management objectives are to: 1) establish sustainable breeding populations of key species; 2) optimise population growth of key species by active management; 3) maintain biodiversity in the park. Key species for the WNP are the white rhinoceros (*Ceratotherium simum*), black rhinoceros (*Diceros bicornis*), roan (*Hippotragus equinus*), sable antelope (*Hippotragus niger*) and buffalo (*Syncerus caffer*). Here, these animals are free of the foot and mouth disease virus (FMDV). The giraffe (*Giraffa camelopardalis*) and eland (*Taurotragus oryx*) serve as breeding stock for reintroduction to other parks.

The introduction of ungulate species into the WNP was done mostly during the 1970s to the early 1980s. The following species were ranked as rare and endangered species in Namibia and were subsequently introduced to the Waterberg National Park: The white rhino was introduced in 1975 and 1976, black rhino in 1989 and 1994, giraffe in 1972, buffalo 1981, roan in 1975 and 1978, sable in 1978, hartebeest in 1974, tsessebe in 1984 (Du Preez, 2001). Unfortunately, the harvesting of most of these species was not well documented from the year of introduction, except for giraffe, of which a total of 67 individuals were harvested between the years 1993-2009, buffalo (80 between the years 2006-2008) and eland (580 between 1989-2009) (Erb, 2009). Some species, such as roan and sable, in which populations showed a decline, cannot be harvested at the current population size, and this was the case since introduction. Other species, *e.g.* hartebeest (*Alcephalus buselaphus*) and tsessebe (*Damaliscus lunatus*) were introduced into the park. However, comparatively less effort is spent on the breeding of these species. Hartebeest are viewed as less important due to their abundance on various game farms, and tsessebe have not bred successfully suggesting that the W.N.P is unsuitable for them as breeding habitat.

5.4 Data Collection

5.4.1 The aerial survey (total count)

The aerial survey was conducted firstly by the Nature Conservation Department (South West Africa) during 1983-1988 before Namibia’s independence, and then by the Ministry of Environment and Tourism of Namibia, (Directorate of Scientific Services) during the years 1997, 2000, 2005 and 2009-2013 after Namibia’s independence. The survey was carried out using a five-seater Bell Jet Ranger helicopter V5-HEM. During the years 1984-1988, the survey was conducted without GPS navigation system. The park was than divided into 25 sectors and each year, counts were conducted over two subsequent days, requiring in total c. 10 hours. The survey was conducted during the morning and early afternoon. The aerial census was held within the same week as ground waterhole counts, i.e. in the month of August. An experienced pilot flew the helicopter together with two observers and one recorder. During a survey, each observer was allocated a 250 m strip width with the aid of the road, 250 m from the flight path of the helicopter and 80 m above the ground. The crew was connected by an intercom system. In order to improve visibility during the aerial survey, all four doors were removed, and the two observers wore ski-masked to protect their eyes from wind. Disturbance of animals during the census was kept to a minimum; animals were not followed. However, because of the altitude, it is not expected to obtain as accurate data on population structure (sex and age structure) as during the waterhole counts.

In the early 1990s, the surveys were conducted using GPS navigation systems (1997, 2000, 2005 and 2009-2013). Custom QBasic software was used to generate the transect lines, spaced

500 m apart over the entire park's surface area. The flight altitude was standardized at 100 m above ground as much as possible. Transects had north-south orientation, except for two areas with rocky gullies, which run predominately in the east-west direction. The beginning and the end point co-ordinates were recorded in ASCII file format. The areas laying below the plateau (Onjoka, Rodenstein) and the isolated Omuverumu Plateau were not surveyed. Transects generated by the software, were loaded into a Garmin 12 XL GPS using Ozi Explorer. One GPS was used for navigation purposes, while waypoints were recorded on a second GPS of the same model. The track plot flown was recorded on both GPS during the flight. During the survey, the observers systematically scanned their allocated strip widths. At each sighting made by the observer, the recorder would note down, waypoint number positioned in the GPS, ungulate species, their numbers and if possible sex and age of each animal.

To ensure the complete coverage of the ground, the pilot and the recorder assisted the observers by counting the animals directly beneath the helicopter. After each survey, the data recorded on the GPS were downloaded to an Ascii file format. Double counts were minimized by: not counting animals moving to the neighboring transects, circling and counting large herds, even slightly off the currently surveyed transect and while evaluating the data, highlighting rhinoceros sightings and attempting to individually identify them, maintaining transect lengths not longer than 10 km to ensure that the observer could remember animals moving to the neighboring transect. All ungulates were counted, with a special attention paid to rhinos and also buffalo, roan, sable or eland. Wherever herds of these species were encountered, the helicopter circled over the herds to obtain precise count and to sex and age the animals, especially rhino. Some bigger herds were photographed for subsequent count verification.

5.4.2 Waterhole counts

Since the Waterberg has a limited number of open waterholes, during the dry season, waterhole count were conducted as another alternative way to count ungulates. The counts were conducted during the years 2009-2013. To increase visibility, waterhole censuses were conducted biannually at the full-moon periods of dry season (June and/or July, and August). Specially constructed counting hides and public viewing hides were used at all seven waterholes. The game was accustomed to the permanent hides. Each counting site was manned by at least two people. The counting and recording of data were alternated between the two every four hours. Each count lasted 48 hours. The counting procedure was conducted simultaneously at all sites. Each data sheet had a serial number in order to facilitate filing. The location and name of the waterhole and observer(s) were recorded.

The following data were filled into standardised data sheets: 1) the time of arrival and departure of animals, as well as directions of arrival and departure; 2) the number, age and sex of the animals in each group, determined as accurately as possible. Regarding the age classes, animals were classified as adult, sub-adult or juvenile. Individuals that could not be assigned to any of these categories, were recorded under ‘unknown’; 3) under the column ‘comments’ the observer(s) noted any particular observations that might help to recognize certain groups or individuals (e.g. details of markings, such as ear tags, collars/neck bands or distinctive characteristics, such as broken or skew horns); 4) in case an animal or group is recognised as one that drank at a particular waterhole previously during the count, it was recorded in the prescribed way but with the addition of a mark next to the new observation.

5.5 Data analysis

Population dynamics for all ungulate species was elaborated using the total counts (aerial surveys), while the correlation between the amount of rainfall (measured from 1st July to 30th June of following year), and the number of individuals of particular ungulate species counted just after this season, i.e. in August/September. In addition to the aerial surveys, water point counts were conducted during the years 2009-2013 to test the difference in the number of ungulates between the aerial counts and water point counts. The dominance of particular ungulate species was calculated as the percentage of the mean number of individuals belonging to this species to the total mean number of all ungulate individuals (except for the black rhino and white rhino) recorded in 11 years (during 1998-2013). The data for rhinos were omitted due to the current policy of a high confidentiality (poaching problems) enforced by the Ministry of Environment and Tourism of the Namibian Government. The regression analysis (regression coefficients, significance levels, relationship graphs and equations) were conducted using Microsoft Excel to generate the relationships between the number of individuals of particular ungulate species and the amount of rainfall.

5.6 Results

During the years 1980-2013, 17 ungulates species were recorded in the this protected area. Two of them, the black rhino and white rhino belonged to the order Perrisodactyla, and the remaining 15 to Artiodactyla. Among the ungulates censused during the years 1998-2013, the most common were the African buffalo and eland, comprising together more than half of all ungulates recorded. Fairly common (each species with 5-12% of all ungulates recorded) were also the roan, sable antylope, kudu and warthog. Four other ungulates, namely the white rhino, black rhino, giraffe, and gemsbok have been classified as uncommon (together 11.9%). The remaining seven species were rare in the WNP (together 1.9%). Among these 17 ungulate species, eight have shown an increase in numbers during the years 1980-2013, six others a decrease, and the populations of two other species remained stable.

The population of the buffalo has shown the most dramatic increase over these years, from a dozen or so individuals in the 1980s to more than 500 in the early 2010s. A similar increase rate was also recorded for the giraffe from a few individuals in the early 1980s to about 200 in the early 2010s. It was difficult to determine population trends for the small antelopes, as they can be easily overlooked during surveys. Collected data suggest a slight increase for the common duiker (*Sylvicapra gimmia*) and steenbok (*Raphicerus camperstris*), and a stable population of the klipspringer (*Oreotragus oreotragus*). While the roan has decreased, the sable antelope have slightly increased in numbers during the years 1980-2013. The eland population remained faily stable, but the related kudu *Strepsiceros strepsiceros* and gemsbok (*Oryx gazella*) have declined. Similarly, the tsessebe population remained stable, but that of related hartebeest dramatically declined. The warthog has dramatically declined in the 1980s but in subsequent years its numbers stabilized on a low level. The decline of the blue wildebeest (*Connochaetes taurinus*) and impala (*Aepyceros melampus*) was so drastic that both species eventually became locally extinct (Table 5.1).

Table 5.1. Ungulate community in the W.N.P during the years 1998-2013 (N = 11 years). x – average number of individuals per year, Var. – variance, %D – dominance (in percentage), SD – standard deviation, Min. – minimum number of individuals per year, Max. – Maximum number of individuals per year. The data for rhinos were omitted due to the current policy of a high confidentiality (as an anti-poaching measure) imposed by the Ministry of Environment and Tourism of the Namibian Government.

Species	x	Var	D%	SD	Min.	Max.
Giraffe	63.8	127935.4	4.7	32.9	5	103
Buffalo	415.4	5026807.4	30.4	248.1	169	1029
Eland	386.4	4812139.7	28.3	128.6	154	537
Roan	174.5	997028	12.8	31.7	131	227
Sable antelope	102.9	364294.5	7.5	29.3	59	145
Gemsbok	29.6	30051	2.2	21.2	5	68
Kudu	82.3	240256.1	6.0	46.3	24	165
Hartebeest	12	4501.3	0.9	7.8	5	25
Wildebeest	1.5	77.3	0.1	0.4	2	3
Tsessebe	4.5	992.1	0.3	8	1	23
Impala	4.4	952.1	0.3		48	48
Warthog	83.3	235174.6	6.1	32.3	19	124
Klipspringer	0.7	26.4	0.1		8	8
Duiker	3.9	451.7	0.3	10.2	1	26
Steenbok	1.6	133.9	0.1	4.5	1	11

During the years 1998-2013, males of the white rhino, black rhino, gemsbok and warthog have increased in numbers faster than females, while the reverse situation was recorded for species such as the giraffe, African buffalo, eland, and roan. In African buffalo and eland, the numbers of observed juveniles increased faster that adults (suggesting increasing population), while the reverse trend (suggesting decreasing population) was recorded for the roan and gemsbok. In other species such differences were minimal (Table 5.2).

Table 5.2. Trends in population growth between males and females, and between adults and juveniles during the years 2008-2013 in Waterberg Plateau Park.

Species	Males		Females		Adults		Juveniles	
	Equation	R^2-value	Equation	R^2-value	Equation	R^2-value	Equation	R^2-value
White rhino	1.4x - 0.6	0.8448	6x - 7.4	0.6777	7.4x - 8	0.7392	3.1x - 3.3	0.6768
Black rhino	5.9x - 4.1	0.8187	7.2x - 6.8	0.7355	13.1x - 10.9	0.7803	3.5x - 3.1	0.7996
Giraffe	5.5x + 9.1	0.3795	6.4x + 0.4	0.5995	11.9x + 9.5	0.5186	4.3x - 0.3	0.4609
Buffalo	37.9x + 28.1	0.4979	73.2x + 37.2	0.5953	111.1x + 65.3	0.5690	56.3x + 1.9	0.7119
Eland	13.3x + 16.5	0.2928	26.8x + 57.8	0.4189	40.1x + 74.5	0.3764	41.3x - 27.9	0.7286
Roan	5.9x + 14.3	0.2780	14.8x + 8.2	0.5772	20.7x + 22.5	0.5164	4.8x + 16.6	0.1381
Sable antelope	0.6x + 10.4	0.0183	-1.1x + 32.05	0.0122	-0.5x + 36.7	0.0009	1.1x + 27.45	0.0047
Oryx	1.1x – 1.1	0.8176	1.1x + 0.3	0.4449	2.2x - 0.8	0.6142	0.077x + 0.46	0.0769
Kudu	-0.6x + 6.55	0.1036	-3.8x + 26.8	0.1933	-4.4x + 32.4	0.1629	1.7x + 7.15	0.1917
Warthog	3x + 11	0.2064	-0.1x + 23.7	0.0001	2.9x + 34.7	0.0406	0.6x + 20.2	0.0037

The comparision between aerial counts and waterhole counts of observed animals between 2009-2013 varried among the different species. In giraffe, sable , gemsbok and hartbeest more numbers were observed at the waterpoints than those in aerial counts. However for the eland, buffalo, roan the aerial counts generated more numbers as compared to waterpoint counts. Kudu trents where not consistant across the years regarless of the method used to sample them.

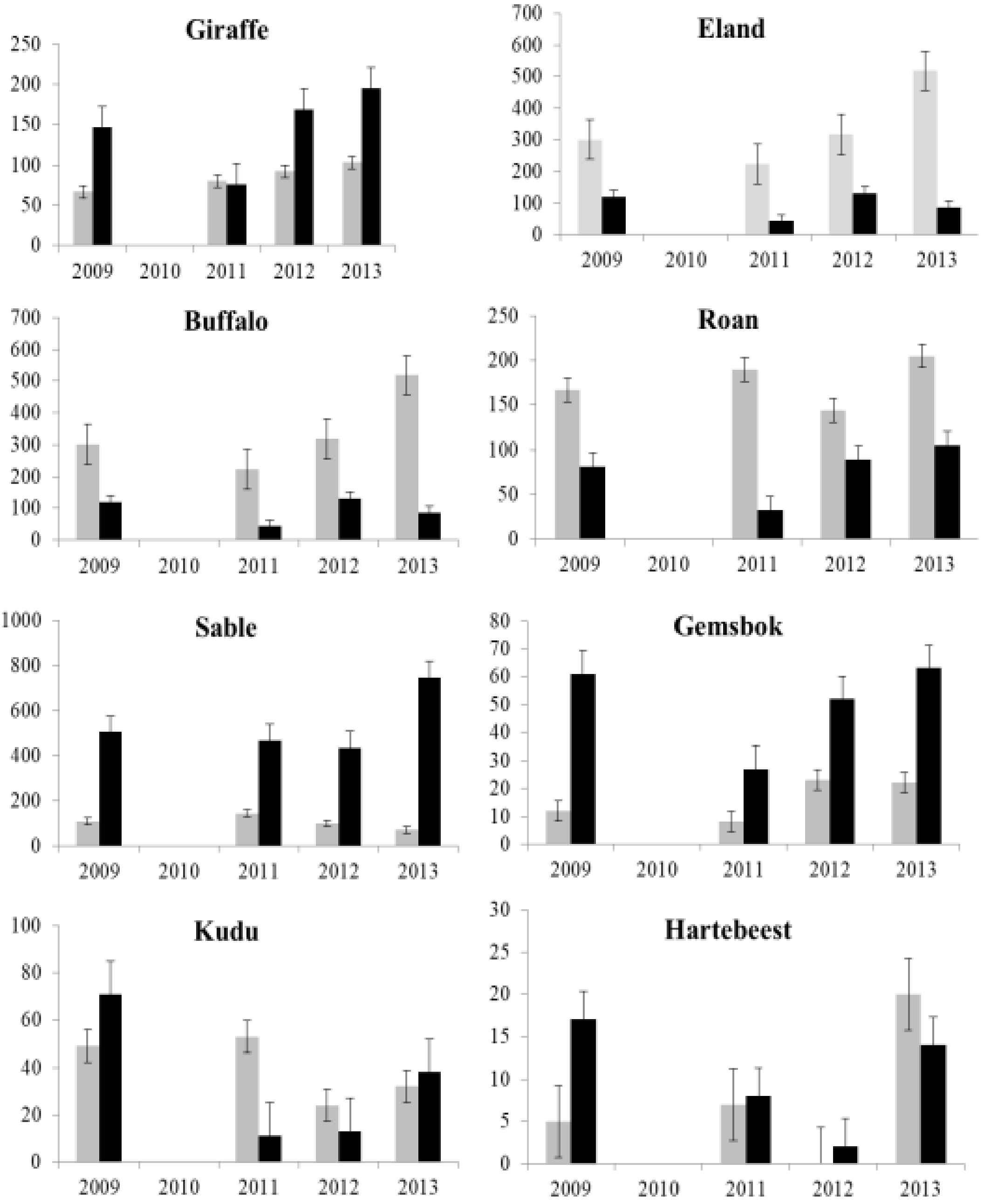

Figure 5.3. Difference in the number of ungulates [vertical axis] between the aerial counts (grey columns) and water point counts (dark columns) in Waterberg Plateau Park in 2009-2013.

For some ungulate species relationships were detected between their population sizes and precipitation. The population of eland (R^2=0.005) was positively but weakly linked with the annual average rainfall between the years 1981-2013, whereas the population of kudu (R^2=0.0456), sable (R^2=0.1697), gemsbok (R^2=0.0275) and roan (R^2=0.0501) were negatively but weakly linked with the amount of rain (Figure 5.4.c, d and g). On the other hand, the populations of giraffe (R^2=0.0039), buffalo (R^2=0.1506) and hartebeest (R^2=0.5083) were not significantly related to rainfall (Figure 5.4 a, b and h). The breaking point of all species densities was in the year 1995, when all species densities decreased dramatically except for buffalo which was only slightly affected. The year 1995 had the lowest rainfall (159mm) during the period 1980-2013 (Figure 5.2 and Figure 5.4). The year 2011 had the highest rainfall (893mm) of the period, but most species densities decreased, whilst all species densities except for hartebeest gradually recovered in the year 2012 onwards (Figure 5.2 and Figure 5.4).

Figure 5.4. Trends in rainfall in (mm) [vertical axis to the left] and the number of animals [vertical axis to the right] during the years 1983-2013 [horizontal axis] in WNP, together with the results of regression analyses.

5.7 Discussion

Historically, vast populations of large herbivores roamed the plains of Africa (Gordon *et al*., 2004; Owen-Smith, 2005), controlled to a large extent by predators, water and forage availability. Currently, many of the species have to be actively conserved in an environment substantially impacted by anthropogenic activities (Gordon *et al*., 2004). Often this modified environment has fewer predators and is water-supplemented. While it is important to understand ungulate population dynamics in a pristine setting, contemporary conservation also requires an understanding that specifically targets these modified settings. In both pristine and modified environments, long-term ecological studies of population dynamics in large ungulates provide a detailed understanding of the intrinsic and extrinsic factors that determine population size and population structure (Gaillard *et al*., 2000). These studies concentrate on the relationships between population density, climate and individual survival rates of different sex/age classes (Gaillard *et al*., 2000).

Coe *et al*., 1976 noted that there is a direct relationship between annual rainfall and abundance of large African herbivores. Large ungulate populations are known to be limited by their food supply (Sinclair, 1974; Coe *et al*., 1976). This suggests that the relationship between rainfall and herbivore abundance operates through the effects of precipitation on primary production. Irregular rainfall and the availability of water in semi-arid environments affects the spatial distribution, quantity and quality of food for large herbivores (Tsindi *et al*., 2016). As illustrated elsewhere, the larger the herbivore species, the more tolerant it is to low quality diet (Bhole *et al*., 2012). Species found in the WNP, such as the white rhino, giraffe, eland, gemsbok and other grazers may benefit from open areas, as long as these areas provide cover and shade, although they differ in their specific dietary needs and preferences. Availability of specific food plants may limit their reproductive success and population growth. Important is both the composition of grass species as well as plant height. The main habitat in the WNP (*Terminalia sericea-Melhania acuminata* – tree-shrub savanna) is dominated by relatively coarse and unpalatable species, particularly (*Eragrostis pallens*) (Chapter 3). With low amount of such preferred palatable species as the black-footed grass (*Brachiaria nigropedata*), bottle brush grass (*Anthephora pubescens*), or crab grass (*Digitaria seriata*), this habitat should be regarded as sub-optimal for the grazers.

The most successful species in the WNP: giraffe, eland and buffalo have a relatively wide dietary spectrum. The buffalo is the only grazer that can cope with denser bush by pushing it aside in order to access the grass (Estes, 1997). On the other hand, the sable and roan antelope are highly selective grazers. They depend on medium to tall climax grass species. Roan feed a wider range of grass species on the plateau than the sable, but both grazers may feed also on a number of same grass species, thus they might compete with each other (Erb, 1993). Those two antelopes may also compete with the buffalo, as it may easily switch to graze on grass species preferred by the roan and sable. Both antelope species appear to avoid competition with the largest grazer, the white rhino. Their preferred foraging habitats (taller grass) are of lower dietary value for the white rhino (chapter 3).

The number of ungulate species in a given area is related mainly to the diversity of habitats, and this, in turn, is often the outcome of the area's size. For example in the Kruger National Park, South Africa (19.6 thousands km^2) there are 16 habitat types and 37 ungulate species; in Kafue NP (24.0 thousands km^2) – 11 habitat types and 30 ungulate species, in Hwange NP (14.6 thousands km^2) – 9 habitat types and 27 ungulates species, while in Etosha NP (23.2 thousands km^2) – 7 habitat types and 24 ungulates species (Grange *et al*., 2012). In the much smaller WNP (405 km^2), with only five habitat types, 17 species were recorded. Elsewhere, the presence of larger water bodies may further increase this diversity, as some ungulate species are strictly water-dependent, e.g. hippopotamus (*Hippopotamus amphibious),* waterbuck (*Kobus ellipsiprimnus),* red lechwe (*Kobus leche),* sitatunga (*Tragelaphus selousi),* or bushpig (*Potamochoerus larvatus*) (Sinibaldi *et al*., 2004). This was, however, not the case in WNP, as there is a lack of permanent water bodies in this area.

In African savanna, rainfall and predation (especially by lions) are widely regarded as the main factor controlling population density of large ungulates (Coe *et al*., 1976, Owen-Smith, 1990, Mills *et al*., 1995, Ogutu & Owen-Smith, 2003). These factors are in some areas interlinked (Mills *et al*., 1995). Rainfall determines vegetation growth and therefore food resources for ungulates (Coe *et al*., 1976). Since grasses respond more steadily to annual rainfall variability, grazers are more directly affected by this variability than browsers (Oguto & Owen-Smith, 2003). The strong relationships between species densities and rainfall in WNP suggest that rainfall does infect control the dynamics of some ungulates, and that changes in rainfall indirectly altered the abundance of these animals (Mills *et al*., 1995; Mduma *et al.*, 1999; Georgiadis *et al*., 2003; Owen-Smith, Mason & Ogutu, 2005; Ogutu *et al*., 2008). The amount of rain in WNP between the years 1980-2013 varied considerably more so between the years 1980-1999, where WNP received most of its rains only during the early months of the year

(January-March). The WNP experienced three years of drought (1995, 2000 and 2013), and received its highest rainfall between the years 2009-2012. While populations of the giraffe and buffalo increased across the years 1980-2013, those of the kudu, sable antelope, roan and gemsbok decreased. Differences in rainfall responses of the grazers to those of the browser and mixed feeders suggests that the influence of rainfall on abundance was not substantially altered by the dietary guild of these herbivores as noted in Ogutu *et al*. (2008).

In the Kruger National Park, the survival of ungulates was subject to past prey availability to main predators and to the effect of preceding rainfall. However, juvenile survival differed from adult survival in most species investigated (Owen-Smith *et al*., 2005). Six ungulate species declined substantially in abundance over the years 1982-1994: kudu, sable, roan, warthog, tsessebe and waterbuck, while populations of zebra (numbers significantly influenced by movements), giraffe, wildebeest and impala were stable (Owen-Smith *et al*., 2005). Those ungulate species with stable populations were not affected by the amount of rainfall, but the decline in kudu numbers was attributed to the outbreak of anthrax and decline in the amount of rainfall. Similarly, the declining population density of the sable and warthog was also attributed to the declining amount of rainfall over the years 1982-1994. Historically, lion predation in Kruger National Park was the main factor responsible for the decline of the roan, sable and warthog. The sable was in addition negatively influenced by dry season rainfall.

In the Hluhluwe-iMfolozi Park, South Africa, population growth rates of seven large ungulate species (giraffe, kudu, impala, nyala (*Tragelaphus angasii*), wildebeest, zebra (*Equus quagga*) and warthog) were in 1986-2010 little affected by both rainfall variation and changes in lion numbers. Only wildebeest numbers were affected by rainfall, and zebra numbers by lion predation (Grange *et al*., 2012). However, in the Kruger National Park, South Africa, buffalo, kudu, roan, waterbuck, and tsessebe populations increased with raising prior rainfall; and populations of the zebra, wildebeest, and giraffe were negatively affected by prior rainfall. The warthog, sable, eland and impala were most abundant in intermediate level of preceding rainfall (Owen-Smith, 1990; Mills *et al*., 1995, Ogutu & Owen-Smith, 2005). While the wildebeest, and to lesser extent zebra, were more vulnerable to lion predation in wetter compared to drier years, the reverse was true in the case of the buffalo and waterbuck, and no effect was recorded in the case giraffe and kudu (Mills *et al*., 1995). In Hwange N.P., Zimbabwe, the relationship between large ungulate densities in the late dry season and the rainfall of the previous rain season, were all negative. However, due to low sample size the correlation was not statistically significant. Possibly, changes in the population dynamics of the elephants affected the numbers more than variation in the rainfall (Chamaille-Jammes *et al*., 2009).

In the Masai Mara National Reserve, and adjoining Koyiaki pastoral ranches in Kenya, the declining pattern of ungulate populations during the years 1977-2008 was consistent with a general declining trends in other protected areas in East Africa (Bhola *et al.*, 2012). This was caused by increasing human settlement and associated poaching, conversion of natural vegetation into arable grounds and competition with livestock and displacement of wild ungulates by livestock incursions into protected areas. The year-to-year changes in the ungulate population densities in the Masai Mara National Reserve differed from those in the neighbouring pastoral ranches. These differences were also related to the body size, feeding guilds and nutritional value of the forage, predation risk and competition with livestock. Small ungulate species were more common on the pastoral ranches than in the reserve (reduced predation risk). Medium-sized herbivores, preferring short grasses, such as zebra, wildebeest and topi (*Damaliscus corrigum*) moved seasonally between the two areas (depending on water and food availability), but medium-sized species preferring long grasses (hartebeest and waterbuck) remained in the reserve. Large-sized herbivores were more common in the reserve than in the pastoral ranches (no need to avoid predators). Although the authors do not discuss the year-to-year variation in the abundance of particular ungulate species in the Masai Mara National Reserve, some pattern are apparent from the presented graphs. Giraffe, buffalo, impala, topi, hartebeest and Thomson's gazelle (*Gazelle thomsoni*) declined, while eland, Grant's gazelle (*Gazella granti*), wildebeest, and warthog populations were stable over the years 1977-2008. Elephant (*Loxodonta africana*), wildebeest and zebra population greatly fluctuated from year to year, with a long-term stable tendency. The annual rainfall averaged 1010 mm, but the authors failed to provide data on year-to-year changes in the amount of rainfall. The long-term declines could be linked to increasing human-induced factors (increased number of people, and livestock) rather than to the amount of rainfall. However, similar tendencies were shown in the reserve and ranch. Larger ungulates are usually more vulnerable to human pressure, but this is also not apparent in this study. This suggests that the main factor responsible for these changes was the amount of rainfall changing from year to year.

In non-protected areas of the Laikipia District, Kenya, changes in the type and intensity of land use were the most important factors controlling population densities of wild ungulates. Rainfall limited densities of only dominant grazing species (i.e. zebra) and other ungulate species which reached high population densities (Georgiadis *et al*., 2007). The breeding success of African ungulates, and therefore population density, can be further limited by amount of rainfall. For example, the roan and sable antelope do not occur in areas that receive less than an average of 400 mm rainfall per annum (Martin, 2003), while the buffalo does not occur in areas that experience less than 250 mm rain per annum (Apps, 2000). The WNP falls within the 500-600mm rainfall isohyet (Du Preez, 2001), and with the mean annual rainfall of 424.5 mm during the years 1981-2001, provide good environmental conditions for these species (Du Preez, 2001). The majority of the key species which reside in the WNP depend on permanent access to water. There are seven artificial waterholes widely distributed over the WNP, which provide good quality water throughout the year. The WNP therefore, fulfils the requirements of all ungulate species which reside there. Nevertheless, rainfall affects ungulates via the availability of food, and via food quality.

To summarise, the population dynamics of ungulates is driven by variations in climate which affects the growth, development, fecundity, and demographic trends of the population (Gedir, 2015). Variations in precipitation affect the production of plant material and indirectly the carrying capacity of the ecosystem in which these animals occur (Coe *et al.*, 1975). Thus, low rainfall restricts plant growth and hence reduces the nutritional value of available plants, whilst excessive rainfall could also be detrimental by favourably promoting the growth of more competitive grasses, higher in fibre content (Ogutu *et al.*, 2015). It was evident in this study that population dynamics trends of ungulates in a water supplemented environment, are in fact indirectly regulated by rainfall, which promotes vegetation growth and hence food production (Rutherford, 1980). The population trends were inconsistent across the different ungulate species mainly due to the fluctuating rainfall but other factors such as competition amongst the grazers may also have influenced the population trends. The temporal pattern of population declines of gemsbok, redhartebeest, roan and sable was consistent with a lagged effect from years of drought or competition for food in addition to the effects of seasonal rainfall. Species that maintained high abundance like the giraffe and buffalo responded mainly to an immediate or lagged density feedback (as in Owen-Smith and Mills, 2006). The population trends of ungulates in WNP were comparable to those documented in other regions of sub-Saharan Africa, while keeping in mind that here the effects of predation were limited to leopards only. Harvesting of game is necessary in the absence of predators as a means of controlling population densities of species that show population growth beyond (or approaching) the maximum ecological capacity of a given park. Thus, we recommend that numbers of harvested animals in WNP should be based on accurate and updated data on population sizes, including demographic profiles (age classes and sex ratio, Chapter 4). These data are necessary to allow objective assessment of harvesting rates. In addition, simulation modelling to project population development over time should be applied (Erb, 2009), including however new rainfall data, and possibly the development of local predator pupulations.

5.8 Acknowledgments

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CHAPTER 6: GENERAL DISCUSSION, CONCLUSIONS AND RECOMMENDATIONS

The monitoring of conservation areas has become more demanding as conservation goals have expended from merely saving rare and endangered species to sustaining biological diversity and the functioning of ecosystems (Poiani *et al*., 2000; Norris, 2012). Understanding population trends, and the factors that are governing both population and ecosystem viability is therefore of outmost importance to planning and managing wildlife populations and the success of alternative conservation policies in general, and specifically so in semi-arid environments (Reynolds *et al.,* 2007). The aim of this thesis was to assess the factors driving the ecological aspects of ungulates in WPN, using different methods for ungulate sampling. In view of this aim, it was essential to investigate varied patterns that would provide insights towards adaptable management and conservation of ungulate species in the park. To achieve this aim, the specific objectives were: 1) to investigate the daily drinking activity pattern of ungulates in the Waterberg National Park in Namibia; 2) to assess the distribution, habitat use and abundance of ungulates across small to intermediate temporal and spatial scales, in Waterberg National Park, Namibia; 3) to assess how population structure differs among species in the Waterberg National Park, Namibia; and 4) to determine population trends of all ungulate species in the WNP over the last 33 years and compare the population trends with those documented in other regions of sub-Saharan Africa.

The daily activity schedules of ungulates reveal how animals cope with changing environmental conditions in securing food and evading predators (Owen-Smith & Goodall, 2014). It has been suggested that ungulates populations limited by the availability of food should maximize their energy in their foraging time allocation, while those controlled by predation should minimize their mobile activity levels (Charnov & Orian, 2006; Favreau, 2014). Arid and semi-arid climates have unpredictable precipitation patterns, therefore, wildlife conservationist provide supplemental water to aid ungulates endure the hottest, driest periods (Gedir, 2016). When surface water is unavailable, the only source of water comes from the forage that they consume, and they must make resourceful foraging decisions to meet their requirements. Winterbach & Bothma (1998) noted that water requirements and its availability may greatly affect the daily activity pattern of some animals and that the effective management depends on the knowledge of such patterns. Ungulates species in this study differed in their water needs in ways that were not necessarily related to their body sizes. Some species were more water-dependent and drank more regularly compared to others (also pointed out in Crosmary *et al*., 2012; Hayward & Hayward, 2012). However, the time of drinking as expected was influenced by the vulnerability to predation which was dependent on the size of the animal. Large ungulate species, like the rhino and buffalo, were mainly nocturnal in their drinking activity while smaller species like the warthog were day-time drinkers. On the other hand, medium-sized species like the roan and sable showed preference to day time drinking activity as also noted by Dery (2016).

Ungulate population sizes are controlled by the availability and quality of forage, and by water availability, both of which can vary spatially and temporally, and which are both dependent on precipitation (Favreau, 2014). Relevant to spatial variation, ungulates can move in the landscape at small scales between different foraging patches, at medium scales across feeding areas, and in migratory species also over larger scales through seasonal migrations (Fryxell and Sinclair, 1988; Favreau, 2014). Forage availability and quality vary seasonally, which can influence ungulates foraging behaviour. More so, in ecosystems exhibiting distinct seasonal variation in forage productivity due to periodic variation in rainfall and temperatures, such as those experienced in African savannas, many ungulates species migrate to areas of better forage quality and availability (Fryxell and Sinclair 1988; Favreau, 2014). Non-migratory species foraging behaviour can also be altered by seasonal forage variation. In these environments, water is scarce and precipitation is unpredictable in timing, amount, and spatial distribution (Schwinning & Sala, 2004; Mwakiwa *et al*., 2012; Gedir, 2016). As a result, there is high variability in the quantity, quality, and distribution of resources that maintain populations (Owen-Smith, 1990; Marshal *et al*., 2005; Bleich *et al*., 2010), and therefore, the distribution of the ungulates in these habitats. The distribution of ungulates is important in shaping vegetation structure and quality of ecosystem function and this can be influenced by the availability of water (Ogutu *et al*., 2010). Even though water availability is considered to be essential in habitats of semi-arid environments, it is but one of a number of factors or resources that can influence distribution and habitat use by ungulates (Bleich *et al*., 2010). Vulnerability to predation, body size, mobility, competition, vegetation cover and feeding guilds of different species of ungulates are all other factors that potentially can contribute to the distribution of ungulates in a given area – and these factors should not be analysed separately, but in conjunction with each other. In this study, the probability of detecting animals model (Chapter 3) showed that the detection probability of ungulates in WNP decreases with increasing distance from the road with an expected cluster size of 3 individuals and this is mainly due to the thick vegetation in the park as noted in Schroeder *et al*. (2014). Large ungulates tended to be in high numbers around waterholes whilst small species were mainly found closer to the road. The habitat use of species within WNP was associated with the presence of particular vegetation types as defined by the underlying geology of the park, the species body size and their distance from the water points. Habitat use as shown by the different species appeared compatible to expectations that species densities would decrease with increasing distance from the water points. Species densities indeed decreased with increasing distance from the water points, more so for the buffalo, roan, sable, giraffe and oryx. The results presented here provide empirical evidence as to which species associate with which vegetation type, and as to their association to the water points from a spatial and temporal perspective in the WNP. Furthermore, the results indicate that ecological processes or habitat characteristics associated with the distribution of water points, act as strong drivers of herbivore distributions in semi-arid African savannas, as also noted by Grant (2011). This is evidenced as consistencies and differences between distribution patterns of herbivore feeding groups (grazers, browsers and mixed feeders) on different geological vegetation types. Water points, especially artificial ones, therefore become features in the landscape that can change the distribution of large African herbivores, even in a landscape where natural water is accessible (Owen-Smith, 1996; Grant, 2011). Extricating factors that contribute most to the multi-species animal distributions in WNP by considering a much larger suite of predictor variables that may influence each species distribution, habitat selection and ungulate abundance and consequently comparing values of those predictor variables with other areas across southern Africa is highly recommended.

Wildlife researchers commonly collect herd composition and age/sex rations to assess the demographic structure of ungulate populations (Bender, 2006). In large herbivores, habitat structure and population density are often reported as major determinants of group size variation within and between species (Marino *et al*., 2014). Previous studies have shown that variations in the abundance of ungulates is linked to the seasons, the presence and abundance of other species, or the availability of resources (Keuroghlian *et al*., 2004; Di Bitetti *et al*., 2008; Pérez-Cortez *et al*., 2012; Reyna-Hurtado *et al*., 2012; Pérez-Irineo *et al*., 2016). The irregular availability of water in semi-arid savannas affects the distribution, quantity and quality of food for large herbivores and hence, influences age and sex structure of herbivores with different dietary requirements across wet and dry seasons (McNaughton & Georgiadis, 1986; Davidson *et al*., 2013; Mduma *et al*., 1999*)*. Hence, understanding the patterns of variation in abundance and community structure and the consequences for species diversity is crucial (Fritz *et al*., 2002; Hutchinson, 1959; Gaillard *et al*., 1998). The population structure of ungulates in WNP in terms of vegetation preference showed that *Terminalia sericea–Melhania acuminata* and *Peltophorum africanum* were the most and least preferred vegetation types respectively. *Terminalia sericea–Melhania acuminata* vegetation contains abundant food resources, since it covers an area the size of all the other three vegetation types put together. In terms of sex structure, the average percentage of males was lower than females except for giraffe, in which sexes were evenly represented. Differences in age and sex structure were nevertheless noted across species. Age and sex structure requires constant monitoring in order to perceive changes in the demography of a population over time; hence, it is advisable to continue monitoring the age-sex structure of the animal populations in WNP so that the long-term trends become evident. The park management can adopt long-term techniques for population monitoring, to obtain this information and facilitate expedient planning.

The use of the field and water point counts yielded no major difference in sampling sizes of most of the species, except for the oryx. Hence, to minimize effort of monitoring, the WNP authorities should rather select one of these methods rather than using both. In order to establish a precise objective for the population sizes or carrying capacity of the different species in the park, studies on the feeding ecology, ecophysiology and market research should be conducted. The feeding ecology study should investigate the diet of grazers and browsers, as well as their preferences for particular plant species with emphasis on inter- and intra- species competition, focusing on the declining species such as the roan, sable, hartebeest and gemsbok. Elsewhere, it has been shown that roan antelope and sable antelopes are ecologically similar (Grant *et al*., 2002, Martin, 2003), both being predominantly grazers and preferring open and wooded grassland savannas. They both have a patchy and discontinuous dispersion as a result of their known habitat requirements, and are both sensitive to disturbances and high predation (Grant & Van der Walt, 2000; Grant *et al*., 2002). In areas like WNP were herds are subject to predation by leopards (especially juveniles), they may be unable to recruit new members or merge with other viable herds. Both these species could be used as a conservation model, determining ecological aspects and population trends of one species may provide insight into the extinction risks faced by the other species. Understanding the interactions between social structure, habitat preference, and external pressures on these two species is thus vital for their effective conservation. This would provide insights into the reasons why these species numbers are stagnant or declining in WNP. Based on these results the conservation authority could establish management strategies to either relocate the affected species or to reduce the numbers of those species that are out-competing the others (e.g. buffalo and eland).

There are a number of factors linked to the population dynamic of species densities in sub-Saharan Africa of which the most significant are rainfall, predation, disease and competition for primary production between the different species and their feeding guilds (Campbell and Borner, 1995; Runyoro *et al*., 1995; Ottichilo *et al*., 1997; Ogutu *et al*., 2003). The fluctuations in rainfall over time plays a crucial role in ungulate population dynamics in African savanna, and should be accounted for before the effects of other factors (such as predation, disease and competition) can be considered (Ogutu and Owen-Smith, 2003; 2006; Owen-Smith, *et al*., 2005; Owen-Smith & Mills, 2006; Ogutu *et al*., 2008). The strong relationships between species densities and rainfall in WNP, suggest that rainfall does infect control the dynamics of some ungulates, and that changes in rainfall altered the species densities of these animals (Mills *et al*., 1995; Mduma *et al*., 1999; Georgiadis *et al*., 2003; Owen-Smith, Mason & Ogutu, 2005; Ogutu *et al*., 2008). In WNP species like the buffalo, giraffe and eland increased from the point of introduction and then persisted at high abundance over this period (1980-2013), whilst others like the roan, sable antelope, gemsbok and hartebeest declined towards critically reduced abundance levels (Owen-Smith & Ogutu, 2003; Owen-Smith & Mason, 2005). The results clearly indicate that rainfall variability contributed to the species densities patterns, but seemed inadequate on its own in explaining the contrasting trends displayed by the different species (Ogutu & Owen-Smith, 2003; Ogutu *et al*., 2008). Hence, the drastic decline in abundance of roan, sable antelope, hartebeest, wildebeest and the gemsbok could be associated with grazing competition pressure by the buffalo and white rhino of which densities increased with increasing rainfall over the years (Macandza *et al*., 2012; Havemann, 2014). The breaking point of all species densities was in the years 1995, where all species densities decreased dramatically except for buffalo which was only slightly affected. This dramatic decrease could be associated with the fact that in 1995, WNP had a drought with the lowest rainfall (159mm) of the period 1980-2013. Variations in precipitation affect the production of plant material and indirectly the carrying capacity of the ecosystem in which these animals occur (Coe *et al*., 1975). Thus, low rainfall restricts plant growth and hence reduces the nutritional value of available plants, whilst excessive rainfall could also be detrimental by preferentially promoting the growth of more competitive grasses, higher in fibre content (Ogutu *et al*., 2015). This could explain why even though the year 2011 had the highest rainfall (893mm), species densities in WNP decreased, except for the buffalo which reached its peak in that year. In conclusion, our findings highlight the influences of rainfall on the species population dynamics in WNP over a period of 33 years. Species responding adaptably to variable rainfall patterns are less likely to be threatened by variation in rainfall due to the effects of global climate change on plant phenology than ungulates species that react negatively to the variation in rainfall. This differential ability to withstand rainfall variation will eventually result in changes in ungulate community composition.). It was evident in this study that population dynamics trends of ungulates in a water - supplemented, disease free environment with little to no predators are in fact indirectly regulated by rainfall, which promotes vegetation growth and hence food production (Rutherford, 1980). The population trends of ungulates in WNP were comparable to those documented in other regions of sub-Saharan Africa, keeping in mind that here the effects of predation were limited to leopards only.

As African wildlife populations – inside and outside protected areas – are declining (Gordon *et al*., 2004; Wilkie *et al*., 2011; Norton-Griffiths, 2000, 2007; Newmark, 1996, 2008; Otichillo *et al*., 2000; Ogutu & Owen-Smith, 2003; Caro & Scholte, 2007; Ogutu *et al*., 2009, 2011; Western *et al*., 2009; Scholte, 2011), ecological studies of ungulates will continue to play an important role in shaping our understanding of factors relevant to their survival (David *et al*., 1999). The realization of this would inform and steer conservation and management decisions for African ungulates, while exemplifying how similar research can aid ungulates dwelling in semi-arid regions and confronting similar conditions, elsewhere (Gedir, 2015). In view of the above, it is expected that the present results will provide baseline ecological data, and motivation for conservation efforts focused on wildlife management strategies that will improve the conservation of the rare species present in the WNP. Beyond this specific application though, it is hoped that the analyses presented here will contribute to a deeper understanding of ungulate ecology. In particular, there is need for policies aimed at conserving wildlife in Namibia and elsewhere to be more sensitive to the interaction of abiotic and biotic impacts such as rainfall, the availability of forage, and interspecific competition. Such interactions are key to successful conservation efforts, and their complexity suggests that often studies specifically performed with the local conditions in mind may be needed.

6.1 References

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