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EFFECTS OF ENVIRONMENTAL CHANGES ON THE ASSEMBLAGES OF EIGHT SYMPATRIC LARGE GRAZERS IN THE MOLE NATIONAL PARK, GHANA

BY

KWAKU BRAKO DAKWA

A Thesis submitted to the Department of Entomology and Wildlife, School of Biological Sciences, College of Agriculture and Natural Sciences, University of Cape Coast in partial fulfillment of the requirements for the award of Doctor of Philosophy degree in Wildlife Management

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DECLARATION

Candidate's Declaration

I hereby declare that this thesis is the result of my own original work and that no part of it has been presented for another degree in this university or elsewhere.

Candidate's Signature.....Date.....25/10/16

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Supervisors' Declaration

We hereby declare that the preparation and presentation of the thesis were supervised in accordance with the guidelines on supervision of thesis laid down by the University of Cape Coast.

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ABSTRACT

The goal of this thesis was to determine the effects of environmental changes on the assemblages of eight sympatric large grazers of Mole National Park (MNP). Transects were surveyed in each of five main habitat types over a one-year period by counting large grazers and measuring abiotic, anthropogenic and grass-related variables. Climate and land cover data time series were analysed for change detection and ARIMA models used to forecast changes up to 2020. Mixed effects and regression models of grazing behaviours were used to identify the environmental factors by which animals selected preferred feeding areas. The results indicated there has been a significant climate change over the period. The mean temperature increased by about 0.7 ^{0}C after two decades and the mean rainfall decreased after each decade. Co-existing large grazers avoided resource use overlaps and competition, but allowed high overlaps and some degree of competition when resources were limited. Larger grazers were more selective for forage than smaller ones and habitat use varied seasonally with different patterns for each habitat type leading to inter-habitat shifts by large grazers. The mean density of grazers ranged from 1.18 ± 0.36 (elephant) to 6.5 ± 0.60/km^2 (kob). Populations showed increasing trends for all the large grazers with the potential for further increases in future. With the weight ratio of 1.40, grazers at MNP were closely packed but several species with similar body weight co-existed within the grazer assemblage. Limiting factors, mainly water, fire and anthropogenic, imposed constraints that resulted in either lack of a clear pattern of abundance, distribution and habitat selectivity or unexplored forage in most seasons. Replication of this study about two to four times is recommended to boost the outcome as information for management planning and action.

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KEY WORDS

Abundance

Climate change

Distribution

Land cover change

Large grazers

Mole National Park (MNP)

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DEDICATION

To my mother, Janet Akua Afumaa,

who never had any formal education

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List of Abbreviations

bdry – Distance away from the Parks Boundary

BTD – Burkea–Terminalia Woodland with *Detarium microcarpum*

BTV – Burkea – Terminalia Woodland with *Vitellaria paradoxa*

BW – Body Weight

CP – Percentage Crude Protein

cty – Distance away from the Community

DOM – Percentage Digestible Organic Matter

ENP – Etosha National Park

GB – Percentage Grass Biomass

GC – Percentage Grass Cover

GG – Percentage Grass Greenness

Id – Identity

IUCN – International Union for Conservation of Nature

HNP – Hwange National Park

KF – Kafue National Park

KNP – Kruger National Park

LnBW – Natural logarithm of Body Weight

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MNP – Mole National Park

OD – Okavango Delta

Water – Distance away from the Nearest Source of Water

WR – Weight Ratio

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CHAPTER ONE: INTRODUCTION

Mole National Park (MNP) was established for the protection and conservation of representative savanna fauna in the northern part of Ghana. Though the herbivorous mammals form the majority of the species richness of the reserve, no previous surveys have specifically assessed the ecology of these herbivores. Wildlife research in MNP is scanty in general including evaluation of population trends and status of lions (Burton et al., 2010), censuses (Wilson, Kpelle, & Agyare, 1993; Mackie, 2004; Bouche, 2006) and a number of community and wildlife conflict issues which remain unpublished. Without research data on abundance, distribution and ecological processes, conservation planning will remain inefficient and ineffective (Bauer, de Iongh, & Sogbohossou, 2010).

Background to the Study

Following the Convention of Biological Diversity, governments all over the world have invested in the development of protected areas (PAs). These are sites protecting biodiversity, natural resources, ecosystem services and associated cultural resources, managed mainly through legal or other effective means (Dudley, 2008). Though there has been a marked improvement in the land area covered by PAs (Jenkins & Joppa, 2009), rates of species decline are still high. PAs are the safest refugia for most large mammal populations in sub-Saharan Africa, but their populations continue to decline because of the changes, mainly climatic and anthropogenic, that influence ecological processes within the PAs (Bartlam-Brooks, Bonyongo, & Harris, 2013). The discourse about how important

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anthropogenic, climatic and other factors are to savanna vegetation, ecology and biodiversity is still ongoing.

One of the most important global environmental changes is land cover change (Turner & Meyer, 1994). We need to know how land cover changes affect and interact with global earth systems by monitoring and documenting what causes the changes, what changes occur, and at what time, place and rates at which they occur (Lambin, 1997). There are diverse ways by which to acquire information for this synthesis and remote sensing has an important contribution. For example, remote sensing has been used in land cover change detection studies at local (such as PAs), regional and global scales from the mid-1970s (Lambin, Geist, & Lepers, 2003). It provides basic datasets, quantitatively and spatially, as information for analysis and interpretation of land cover changes, which will be useful for regional, national and local or PA decision-making processes and planning. With remotely sensed data and the application of Geographic Information Systems (GIS), mapping generates statistical estimates for modeling as well as monitoring change detection (Morain & Klankamsorn, 1978; Woodwell et al., 1984; Myers, 1988; Sader & Joyce, 1988; Gilruth, Hutchinson, & Barry, 1990; Green & Sussman, 1990). Landsat satellite imagery is one of the tools used for mapping and monitoring land cover changes (Congalton, 1996). Its association with ground-truth surveys facilitates accuracy assessment for classified satellite imagery (Congalton). Ground truthing may refer to a process in remote sensing in which a chosen pixel on a satellite image is compared to what is on the ground in reality currently, in order to verify and validate the contents of the pixel on the

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image. For a classified image, it helps to determine the accuracy of the classification performed by the remote sensing software in the unsupervised mode and therefore minimize errors in the classification (Cheng et al., 2013).

Predicting the distribution of wildlife populations is an important component of the development of management strategies for their conservation. Landscape structure and composition determine species occurrence and population viability. In particular, extent of habitat richness and its suitability can determine the distribution and abundance of biological populations (Fahrig, 2003). Anthropogenic impacts, such as wildlife mortality through poaching, or human interference through encroachment can also have large impacts on the distribution and abundance of a species (Fahrig, Pedlar, Pope, Taylor, & Wegner, 1995; Woodroffe & Ginsberg, 1998). Therefore, if we are to manage landscapes to conserve wildlife, it is important that we understand the role of these landscape processes in determining their distributions.

Mixed effects and regression models of grazing behaviours can help identify the environmental factors by which animals select preferred feeding areas (Senft, Rittenhouse, & Woodmansee, 1983; Redfern, Grant, Biggs, & Getz, 2003), providing important information about the factors determining the observed distribution patterns of species or guilds of species. The role of biotic factors such as forage quality and quantity in herbivores distribution on landscape have been well documented (Redfern et al., 2003). However, Bailey et al. (1996) suggested that abiotic factors, such as slope, altitude and distance from water, are

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equally important as determinants of large scale distribution patterns of herbivores.

Formulation of proper wildlife conservation and management strategies requires reliable data and information on their numbers, distribution and ecology. These data and information are normally collected using both aerial and ground surveys. Aerial survey involves use of light aircraft to collect data and information on animal numbers and distribution (Norton-Griffiths, 1978; Caughley & Sinclair, 1994). Ground survey methods include direct observation, direct or indirect counts and mapping based on either particular area units, blocks, transects or quadrats (Riney, 1982) to provide data and information on population ecology and mammalian behaviour. Aerial survey methods include direct observation and photography to provide data and information on the abundance and distribution of mammals (Norton-Griffiths, 1978; Caughley & Sinclair, 1994; Seber, 1996) in relation to the environment. Ground surveys tend to be most efficient and cost effective when used for smaller areas. However, aerial methods survey large areas in a short time and may be more efficient, cost effective and easy for surveys where access on the ground is difficult. Data and information from both ground and aerial surveys have been used for different purposes in wildlife management. For example, abundance and distribution data have been used to plan the optimum boundaries of national parks and reserves, to predict species response to environmental disturbances and to monitor wildlife population trends (Western & Grimsdell, 1979). These are also important in formulation of

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comprehensive conservation, management and monitoring strategies for wildlife (Western & Grimsdell).

The high species richness of African grazer assemblages has raised curiosity about the occurrence of so many species of grazers in the same area while using grass as the same resource. Based on classical competition theory, it has been suggested that in herbivore communities differentiation in body size may be a major mechanism permitting co-existence. Indeed, there may even be facilitation, where one species' activities makes food resources available to another which would otherwise be inaccessible or underutilized. When species are very similar in body weight, competitive displacement may occur, whereas facilitation may occur when weight differences are larger but not too large (Hutchinson, 1959; MacArthur & Levins, 1967). Hutchinson observed that character displacement among sympatric species leads to sequences in which each species is roughly twice the mass of the next (weight ratio (WR) theory). Since Hutchinson's weight ratio theory, body size has been used widely as an explanatory variable predicting animal abundance and patterns of assembly (Damuth, 1981; Schmidt-Nielsen, 1984; Fa & Purvis, 1997). Based on the Hutchinson's weight ratio theory, Prins and Olff (1998) hypothesized that in a functional group, facilitation is more likely to occur at a weight ratio (WR) > 2.0, competition at WR < 2.0, while coexistence will occur at WR = 2. Prins and Olff further hypothesized that when species are too similar in body mass, they might not profit sufficiently from facilitation interactions, and competition will occur; and that when species are too different in body mass, the larger herbivore will

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alter the grass quality such that it is unsuitable for small herbivores to use. In this case facilitation will not occur. May (1973) hypothesized that complex or highly heterogeneous systems are expected to support a higher diversity and hence high degree of species-packing, while simple or homogeneous systems are likely to support low species diversity and hence low degree of species-packing.

Body mass is also thought to account for grazing distribution independently of competition or facilitation effects. It has been proposed that herbivore nutritional ecology is related to body size (Illius & Gordon, 1992): ungulate gut capacity increases linearly with body mass (Demment & Van Soest, 1985), and energetic requirements of herbivores are also linked to body mass (Van Soest, 1996). All these are thought to have resulted in strategic feeding allometry (Illius & Gordon, 1987) in which large-bodied animals can process large quantities of low quality forage (Codron et al., 2007), whereas small-bodied animals need to feed selectively on smaller quantities of high quality forage (Janis, 1976) to meet comparatively larger energetic demands (Demment & Van Soest). Larger animals can therefore explore a greater variety of habitat types (Du Toit & Owen-Smith, 1989), resulting in a more widespread distribution (Cromsigt, Prins, & Olff, 2009). Body size also affects the scale at which animals respond to forage heterogeneity (Du Toit & Cumming, 1999). Small animals increase their selectivity when resources are finely interspersed, whereas large bodied herbivores feed indiscriminately on such patches (Laca, Shipley, & Reid, 2010). Predation pressure is not equal for all herbivore species (Mills, Biggs, & Whyte, 1995; Hopcraft, Olff, & Sinclair, 2010); body size is an important factor

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(Cohen, Pimm, Yodzis, & Saldana, 1993) determining the range of potential predators (Sinclair, Mduma, & Brashares, 2003). Most predators prefer particular prey species (Owen-Smith & Mills, 2008), but small herbivores are more vulnerable than large-bodied herbivores because they are easier to capture and kill (Hopcraft, Olff, & Sinclair).

Statement of the Problem

At MNP, research data are scarce, particularly on (a) climate and land cover changes and their effects on the vegetation; (b) species abundance and population dynamics; (c) interspecific herbivore-herbivore interactions and assembly patterns; and (d) spatio-temporal distribution are scarce, but these are needed to formulate a management plan to serve as a guideline for effective conservation action.

Climate-driven fluctuation characteristics of savanna ecosystems make it difficult to investigate causal relationships of land cover changes in short-term studies (Serneels, Said, & Lambin, 2001). However, failure to understand how climate influences land cover change processes limits the ability to manage PAs (Bartlam-Brooks et al., 2013). Despite this, the effects of climatic and other factors shaping the vegetation of MNP have not been studied. Change detection is also important for the management of PAs, as this provides information on change dynamics of the vegetation of the area, which could be a useful indication of the effect this could have on the population of wildlife that depend on the vegetation. However, there are no quantitative data for change detection at MNP.

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Aerial surveys of the MNP were conducted by Wilson et al. (1993), Mackie (2004) and Bouche (2006). The reliability and accuracy of aerial survey data are influenced by various factors. These include the problem of controlling errors due to sampling procedures and accuracy of human observers and bias in spotting and counting animals (Norton-Griffiths, 1978). Whereas it is impossible to eliminate bias from aerial surveys, this can be minimised at the design stage and partially corrected after survey (Norton-Griffiths). Nevertheless, aerial surveys have been carried out to estimate mammalian populations at least three times at MNP yet ground surveys have not been implemented through research; data exists only based on sightings made by field staff during regular law enforcement patrols throughout the park (Jachmann, 2002).

Despite criticisms (Simberloff & Boecklen, 1981), the body weight ratio concept is among the most promising and interesting concepts for furthering understanding of interspecific herbivore-herbivore interactions, even though it is by no means clear yet at which level of relative abundance coexistence, facilitation and competition may occur. In many herbivore communities, coexistence has been observed among ecologically similar species, especially grazers. Also, a high level of resource use overlap has often been used to infer that competition is occurring (Jenkins & Wright, 1988), which also implies that a low level of resource use overlap infers that competition is not occurring. A high degree of overlap may equally well indicate an absence of competition, permitting a sharing of common resources (Gordon & Illius, 1989; Putman, 1996). Despite the importance of species-packing and resource use overlap, these concepts have

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never been evaluated at MNP and so it is not known whether there is coexistence, facilitation or competition among sympatric species of large grazers at MNP. Sympatric species are related species or populations occurring within the same geographical area. Such large grazers as elephant (*Loxodonta africana*), buffalo (*Syncerus caffer*), roan antelope (*Hippotragus equinus*), waterbuck (*Kobus defassa*), hartebeest (*Alcelaphus bucelaphus*), kob (*Kobus kob*), warthog (*Potachoerus aethiopicus*) and bushbuck (*Cephalophus scriptus*) living in the MNP are sympatric.

If we are to manage landscapes to conserve wildlife, it is important that we understand the role of these landscape processes in determining their distributions. For example, understanding the characteristics of ecosystems, in particular the composition of vegetation communities, their productivity and distribution is important to determine habitat selection and use by large grazers, especially for foraging purposes. Determination of habitat selection and use by grazers is a crucial step in studying the relationship between patterns of distribution of animal species. This often involves isolating and measuring vegetation characteristics of an area and relating it to estimated numbers of grazers across sites (Jacobs, 1974; Ben-Shahar & Skinner, 1988).

Theoretically, in an environment entirely free of constraints, one would expect grazers to locate themselves where they are able to maximize their energy gain in the shortest possible time (Bergman, Fryxell, Gates, & Fortin, 2001). For example, Bailey et al. (1996) suggested that large herbivores should spend most time in areas where the available quantity and quality of forage is highest; though

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Bennitt, Bonyongo, and Harris (in press) highlight the importance of other behaviours such as resting to habitat use at different scales, which could influence the functional value of different sites. However, even in PAs, human activities may interfere with animal distributions and may restrain wildlife from using critical habitats (Corfield, 1973; Williamson, Williamson, & Ngwamotsoko, 1988). Additionally, there may be natural restrictions on distributions, such as an overall scarcity of forage, the availability of water, competitive interactions with other wildlife and the effects of predation (Sinclair, 1985; Fryxell, 1991). Thus it is envisaged that a combination of both biotic and abiotic factors in the local environment may be particularly important in determining the distribution patterns of large herbivores in African savanna ecosystems, as argued by Redfern et al. (2003). However, the relative importance of these factors has not been quantified, particularly in reserves, such as MNP, that are also subjected to heavy pressure by human communities living at their fringes.

Purpose of the Study

The purpose of this study was to quantify the abundance of large herbivore grazers, their interspecific interactions, and community assembly patterns in relation to environmental changes in Mole National Park, Ghana's largest wildlife reserve. Such data are essential for formulating a management plan for effective conservation.

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Research Objectives

My overall aim was to determine the present population densities and assembly patterns of eight sympatric large grazers (elephant, buffalo, roan antelope, waterbuck, hartebeest, kob, warthog and bushbuck) within the MNP and to investigate which factors regulate the abundance and distribution of these herbivores.

Specific objectives were to:

1. determine climate and land cover changes in the Park over a 30-year period, forecast changes in the next 10 years, determine the effects of such changes on the densities and distributions of the large grazers over the period and predict the effects of such changes on the densities and distributions of the large grazers over the forecast period.
2. determine the densities and hence estimate thepopulations of elephant, buffalo, roan antelope, waterbuck, hartebeest, kob, warthog and bushbuck and evaluate the trends of population growth with data from past censuses;
3. establish the patterns at which the eight large grazers responded to seasonal resource heterogeneity through their habitat selectivity and use;
4. investigate effects of seasonal variation on quality and quantity of grazing resources and how large grazers respond to the swelling and shrinking of their grazing resources induced by seasonal weather changes;

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5. investigate whether grazers' communities of MNP conform to the Hutchinson's Rule (i.e. body weight ratio of ~ 2.0) and determine what factors allow co-existence of grazers of similar sizes in MNP;
6. determine the effects of body size of the large grazers on resource use in relation to the dynamics of resource availability and distribution;
7. determine the factors that affect the distribution and abundance of the eight large grazers in the MNP and investigate whether some of the variables impose spatial constraints against the selectivity, abundance and distribution of the large grazers.

Research Questions

The hypotheses of this study are based on observations and research questions.

1. Has land cover of MNP changed over the last 30 years? Is this change related to climate change? How have these changes affected the large mammals of MNP?
2. What is the trend of population growth for large mammals studied? What accounts for the trend?
3. What are the patterns of large grazers' resource selectivity and use in the MNP? Do patterns of habitat use by different large grazer species differ seasonally? If so, why do they differ?
4. Does forage quality or quantity vary with the season? If so how do large grazers respond to the swelling and shrinking of their grazing resources induced by seasonal environmental changes?

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5. Do grazer communities of MNP conform to Hutchinson's Rule (a body weight ratio of ~ 2.0)? According to the theory of limiting similarity, competition prevents co-existence of species that are morphologically too similar, so how do the large number of similar sized grazer species in MNP co-exist? If so, what accounts for co-existence in grazer community assemblage?
6. Do habitat resources in the Park support high biomass density? How does difference in body size of the large grazers vary with their abundance, distribution and resource use patterns?
7. Are the abundance and distribution of the large grazers affected by limiting factors that impose spatial constraints? If so, how have the large grazers responded to these spatial constraints in relation to habitat availability?

Hypotheses

I hypothesize that:

1. land cover change at MNP is not due to climate change alone; and that land cover changes affect the densities, abundance and distribution of the different species of mammals in ways related to their habitat requirements.
2. despite poaching reports, the populations of the large grazers are increasing, though population trends of different species vary because of differences in responses to environmental variations and differences in

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recruitment rates; and that population increases may be due to availability of a large carrying capacity resulting from intensive poaching previously.

3. there are clear patterns of resource selectivity because of habitat and forage heterogeneity and the impact of distinct seasonal variations on the habitats; and that patterns of habitat selection and use differ with seasons because of seasonal variations in grass (forage) availability, quality and quantity.
4. forage quality is high during the rainy and flood seasons and low during the dry and fire seasons but forage quantity is abundant during the rainy and dry seasons and shrinks during the fire and flood seasons; and that there are high resource use overlaps among co-existing grazers when forage is low in quality and quantity and low overlaps when forage is high in quality and quantity.
5. the grazers at MNP are closely packed (WR < 2.0) or are too similar in body weight to co-exist and that species are packed closer or wider if environmental variations are smaller or larger respectively; and therefore habitat diversity is the decisive factor in allowing co-existence and grazer community structure.
6. there is interspecific decrease of food quality with increasing body mass in MNP and that grazers with larger body sizes are less abundant, less selective and prefer forage with high quantity than forage with high quality but grazers with larger body sizes are more abundant, more

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selective and prefer forage with high quality than forage with high quantity.

7. water and fire are limiting factors in the dry and fire seasons and so large grazers are most abundant near water sources, and that fire causes forage shrinkage that induces high resource use overlaps. Also, anthropogenic factors impose distribution restrictions as large grazers tend to locate at places far away from nearby communities. For these reasons, a large percentage of habitat availability in MNP remains unselected by the large grazers.

Significance of the Study

This project will provide important information on the population structure and optimal resource characteristics for each key large grazer species. This information will increase our ability to predict how the ecosystem's grazers will be affected by potentially destructive disturbance and can therefore be used to model future populations and develop valuable management and conservation protocols. Apart from the need to develop effective management planning to protect and conserve representative savanna fauna, the large grazers are the main drivers of tourism at MNP and so their conservation is of utmost importance.

Delimitations

The study was confined within the landscape of Mole National Park only, but because some of the grazers, notably the elephant, are known to have home ranges beyond the boundaries of the Park, their distribution could also be

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influenced by factors including type of farm crops outside the Park. The study was also unable to sample the entire area of the MNP landscape due to accessibility and logistic reasons.

Limitations

The main limitation of the study was lack of temporal dynamics as the study took place over only one annual cycle. A study like this would be strengthened by replications over two to five more years to test the significance of temporal trends as this would inform justified conclusions.

Organization of the Study

This thesis consists of six chapters which start with an introduction (chapter one), which includes the justification, objectives, research questions and hypotheses of the study. Chapter two provides a literature review and chapter three describes materials and methods that were used across the thesis, the study area and data management and analyses. Chapter four presents the results and chapter five provides discussion of the results. Chapter six draws conclusion on the major outcomes of the research and provides some recommendations.

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CHAPTER TWO: REVIEW OF RELATED LITERATURE

Introduction

This chapter provides information about previous research related to this study, which also highlight the underlying concepts of the study. It includes information on how the distribution of herbivores are affected by climate and land cover changes globally, and resource use challenges to populations and communities of herbivores including competition and effects of some limiting factors.

Global Distribution of Herbivorous Mammals

Many researchers have reported on the ecology of herbivores including their geographic distribution (Schall & Pianka, 1978; Delany, 1982; Prins & Olff, 1998) and diversity patterns (Hutchinson & MacArthur, 1959; MacArthur, 1965; Pianka, 1966; May, 1986; Hubbell, 1997). It is thought that some geological and geomorphic events might have altered landscape characteristics, which affected the distribution and abundances of animals and their use of habitats over landscapes (Delany). There are six geographical regions in the world based on the distribution of animal species in relation to the different physiographical areas (Delany); and zoological events of the Pleistocene are thought to be responsible for the current distribution and abundance of animal species in these regions (Owen-Smith, 1987; 1989; Morrison, Marcot, & Mannan, 1998). Schall & Pianka named the regions as (1) Palaearctic Region (the largest, covering Europe, Asia and North Africa; (2) Nearctic Region (North America); (3) Neotropical Region

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(extending from South and Central America to Mexico where it meets the Nearctic Region); (4) Ethiopian Region (from south of the Atlas Mountains to the southern tip of Africa, including the islands of Madagascar and part of the Arabic Peninsula); (5) Oriental Region (including Asia south of the Himalayas and a line extending south-east from them to the shores of China Sea), and (6) Australian Region (which includes Australia and its offshore islands, as well as those of the East Indies). During the Pleistocene, a series of events, characterized mainly by oscillations of the continental ice sheets and glaciers, decimated animals and plants in the Northern continents (Morrison et al, 1998).

When the Northern continents returned to ideal conditions such as suitable temperature for the animals after the ice ages, barriers of sea, mountain and desert prevented animals from returning northwards. Consequently, the rich biota of the tropical and subtropical regions (including Africa, India, South-East Asia and South America) are very much different from the biota of Eurasia and North America (Morrison et al, 1998). Of the six zoogeographical regions tropical Asia and Africa have the greatest species richness (Delany, 1982) and African herbivore communities have at least twice the species richness of those of other biogeographic regions (Owen-Smith, 1987; Prins & Olff, 1998; Fritz, Duncan, & Gordon, 2002).

Tropical Savannas

The tropical and subtropical savanna biomes in Africa are extensive with high ungulate species richness (Hirst, 1975), and most of the present ungulate

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species can be traced back to the Pleistocene, or the Pliocene (Wells, 1962, Cooke, 1963). Fossil and other evidences suggest correlation among many forms of ungulate species and major vegetation types such as desert, forest, and savanna (Ewer & Cooke, 1964).

Tree-grass co-existence

About 20% of the earth's surface and about 40% of Africa consist of savanna biomes (Scholes & Archer, 1997). Savanna ecosystems are characterized by a continuous grass layer intermixed with a discontinuous layer of trees and shrubs, which are determined by many and complex interacting factors (Bond & Van Wilgen, 1996, Scholes & Archer), resulting in various changes in the savanna vegetation structure (Jeltsch, Weber, & Grimm, 2000). For example, serial effect of the mount of rainfall determining grass biomass productivity (i.e. fuel load) and frequency and intensity of fire (affecting establishment of grass, trees and shrubs) contribute to savanna vegetation dynamics. As various life stages of plants require certain amounts of rainfall, changes in rainfall patterns may affect the population dynamics of most plants (Tews & Jeltsch, 2004). In tropical and sub-tropical savannas, high temperatures may reduce seasonal rainfall distribution (Scholes & Archer), making water stress in savannas a common phenomenon. The coexistence of trees and grasses is made possible because while water is a limiting factor for both grassy and woody plants, grasses use moisture from the top soil while trees use moisture from the sub-soil (Walker, Ludwig, Holling, & Peterman, 1981; Walker & Noy-Meir, 1982; Eagleson & Segarra, 1985). However, Jeltsch, Milton, Dean, and van Rooyen (1996) showed that

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rooting-niche separation alone may not account for tree-grass co-existence but other factors including ecosystem disturbances, mainly fire, human impact or grazing are key determinants of savannas. They also indicated that savannas are inherently unstable ecosystems oscillating between tree dominance and grass dominance without leading to stable grasslandsor forests, respectively, due to the disturbances (Scholes & Archer; Jeltsch, Milton, Dean, van Rooyen, & Moloney, 1998; Jeltsch et al., 2000; Higgins, Bond, & Trollope, 2000; Sankaran, Ratnam, & Hanan, 2004). For example, overgrazing allows trees to invade grassland, inversely, fire consumes trees allowing grass to invade open areas. Jeltsch et al. (1998) and Rodriguez-Iturbe, D'odorico, Porporato, and Ridolfi (1999) suggest that spatial variation in distribution of seeds combined with low tree recruitment probabilities and high grass establishment potential, could account for the large expanse and persistence of savannas.

Effect of fire

The importance of fire in characterizing vegetation types across landscapes and ecosystems has been widely reported (Stander, Nott, & Mentis, 1993; Parr & Chown, 2003) and, together with climate, soils and grazing, fire determines the structure and function of savanna communities (Skarpe, 1992; Hobbs, 1996; Bond & Keeley, 2005). Climate and fire act in synergy to influence nutrient recycling, vegetation composition and distribution of organic matter (Wessman, Bateson, & Benning, 1997), sward structure (Van De Vijver, Poot, & Prins, 1999) and phytomass (O'Reagain & Owen-Smith, 1996) and therefore forage quality and quantity for herbivores (O'Reagain & Owen-Smith; Durant,

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Fritz, & Duncan, 2004). Fire makes food supply for large herbivores available at different spatial and temporal scales, and so the foraging behaviour of herbivores also differ (Augustine & McNaughton, 1998; Fortin, Boots, Csillag, & Remmel, 2003; Skarpe, Jansson, Seljeli, Bergström, & Ŕøskaft, 2007).

In accordance with the optimal foraging theory (Pyke, Pulliam, & Charnov, 1977; Belovsky, 1984), which predicts that herbivores will maximize the intake of digestible energy and nutrients per unit of time, some herbivores may opt to sacrifice food quality for quantity (Banyikwa, 1976; Senft et al., 1987). Forage quality tends to decline with increasing standing phytomass (Distel, Laca, Griggs, & Demment, 1995; Wilmshurst, Fryxell, & Hudson, 1995; Wright & Illius, 1995) and sward height (Kenney, Black, & Colebrook, 1984; Wallis de Vries, Laca, & Demment, 1999; Wilmshurst, Fryxell, & Bergman, 2000; Fryxell, Wilmshurst, & Sinclair, 2004). McNaughton (1985) proposed that burning in savanna is followed by a rapid increase in phytomass, but this is lower in quantity than in non-burnt grass (Bond-Lamberty, Wang, & Gower, 2004). The quality of grass after burns depends largely and directly on the concentration of nitrogen in live leaf (Prins & Beekman, 1989; Cook, Hershey, & Irwin, 1994). It has been widely reported that in savanna, wild large herbivores patronize burnt areas more than non-burnt areas (Moe, Wegge, & Kapela, 1990; Pfeier & Hartnett, 1995; Tomor & Owen-Smith, 2002). However, based on the forage maturation hypothesis (Fryxell, 1991; Wilmshurst et al., 1995), it is expected that the quality of grass forage will change with time since the burning. At early stages, grass forage has high quality but low quantity; with time, nutrient concentration (Van

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de Vijver et al., 1999) and greenness of the phytomass (Fryxell) decline but grass phytomass increases and, thus, a corresponding change in the selection and use of burnt and non-burnt patches as time progresses is very likely.

Effect of climate

Rustad et al. (2001) predicts a change in the balance between the flora and fauna that characterize tropical savanna communities due to climate change and an increase in carbon dioxide and is likely to change the current distribution of plants and animals. As vegetation is a key variable of interaction between the land and atmosphere, vegetation is likely to be sensitive to climate change, but this depends on the region under consideration (Rustad et al.).

While precipitation change and warming are the most important climatic factors that control ecosystem function and species composition of savanna in temperate systems, CO_2-fertilisation, herbivory and fire regime are the controllers in tropical systems. Little is known about the ecosystem responses to the effects of global warming, rainfall change and change in carbon dioxide level through experiment (Rustad et al., 2001); few data are available only for the experimental assessment of ecosystem responses to multi-factorial treatments (Norby & Luo, 2004). But these factors are likely to affect tropical savanna systems. For example, reduced rainfall reduces vegetation cover and productivity and its sustained form instigates a drying trend that sharpens aridity gradient (Woodward & Lomas, 2004). Conversely, there is subsequent regeneration during wetter periods (Hiernaux & Turner, 2002). Savanna vegetation, in turn, can also

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feedback to rainfall patterns. With an extensive, large-scale vegetation cover, there is increase in the amount of rainfall regionally. Rainfall following a long period of drought in an African savanna system is thought to trigger substantial soil respiratory activities including carbon losses (Veenendaal, Kolle, & Lloyd, 2004), indicating a strong response to rainfall variability. Few researchers have reported on the impact of climate change on savanna and grassland fauna, but Thuiller et al. (2006) suggest the possibility of the proportion of threatened mammal species rising from about 10 - 40% between 2050 and 2080.

Land Cover Change and Detection

Land cover is defined, simply, as the kind and state of vegetation, but it has evolved to include human structures and other aspects of the natural environment (Turner & Meyer, 1994). In this case, buildings, pavements, soil type, biodiversity, surface water, and groundwater form part of land cover reflecting the ecological state and physical appearance of the land surface (Turner & Meyer; Geist & Lambin, 2002). Changes in land use types often result in land cover changes; and human activities dominate the land use types, which therefore are the most influential causes of land cover changes (Turner & Meyer) and the greatest threat to ecological systems (Foody, 2003) that justifies the introduction of current strategies for managing natural resources and monitoring environmental changes (Brandon, 2001). Land cover changes, in turn, impact on global climate and the biosphere by the effect they have on biodiversity, water and radiation budgets, trace gas emissions and other processes (Brandon).

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Land cover changes in PAs could have far reaching implication for wildlife conservation as PAs provide refuge, forage and water resources, breeding grounds, and mating opportunities for wildlife (Newmark, 1993; Okello & Wishitemi, 2006). Land cover may be defined in terms of vegetation, which is thought to play important roles on the earth's surface as indicator for land condition, limiting factor to stocking in managed grazing lands and controller of evapotranspiration, infiltration, run-off and soil erosion (Booth & Tueller, 2003; Bastin & Ludwig, 2006) and therefore changes to vegetation cover leads to changes to the aforementioned processes and effects. Hence, vegetation cover is considered the key indicator in the remote sensing of the land condition.

Remote sensing techniques for assessing land cover changes

Due to the advent and advancement of remote sensing - GIS technology, it is now possible to detect, assess and monitor changes of the earth's surface as these produce satellite imagery that can be interpreted quantitatively (Deer, 1995). Remote sensing is currently the most effective tool and thus a major source of data for different change detection applications. It is capable of repetitive data acquisition, compatible with computer processing and cheaper than those associated with traditional methods (Coppin, Jonckheere, Nackaerts, Muys, & Lambin, 2004; Deer). Change detection is the process of identifying difference in the state of an object or phenomenon by observing it at different times (Deer). It involves the use of GIS in a computer environment to evaluate and analyse multi-date images produced by remote sensing (Lu, Mausel, Brondizio, & Moran, 2004). Change detection is used to evaluate (i) land use and land cover change,

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(ii) forest and vegetation change, (iii) forest mortality, defoliation and damage assessment, (iv) deforestation, regeneration and selective loggingwetland change, (v) forest fire, (vi) landscape change, (vii) urban change and environmental change (Coppin et al., 2002; Cordeiro & Howe, 2003; Foody, 2003; Lu et al., 2004; Mundia & Aniya, 2005; Muttitanon & Tripathi, 2005).

Remote sensing for ecosystem management

Ecosystems render various services that meet human needs, which attract development priorities without paying much attention to the consequences of human actions to the ecosystem structures and health (Congalton, 1996). One of the advantages of the use of remote sensing is its continual advancement to improve the quality and accessibility of important spatial information for natural resource management and conservation. These technological advancements in remote sensing are responses to the growing concerns about the increase in adverse environmental conditions. Geographic Information Systems (GIS) also evolved correspondingly, allowing effective environmental assessment through processing of large quantity of quality data that reflect reliable change detections generated through remote sensing (Lu et al., 2004). As changes in land cover result in changes in radiance values, another promise in using remote sensing data for change detection is that radiance changes caused by other factors such as differences in atmospheric conditions, differences in soil moisture and differences in sun angles are less important as compared to radiance due to land cover (Mas, 1999).

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Time series based land cover change detection

Time series analysis of land cover change and the identification of the driving forces responsible for these changes are needed for the sustainable management of natural resources and also for projecting future land cover trajectories (Cohen & Fiorella, 1998). Much prior work in change detection has often been performed by comparing two or more images of different dates, or snapshots, but this is unsuitable for global analysis and so most of such studies have focused on relatively small areas or specific interests (Townsend & Justice, 1986; Cohen, & Fiorella). Recent works have used time series approaches to detect land cover changes (Roy, Lewis, & Justice, 2002). The use of time series based change detection has significant advantages over the comparison of snapshot images of selected dates because detections of changes are based on observations of the landscape over time and therefore provide information about the temporal dynamics of landscape changes and additional parameters such as the rate, speed, extent and pattern of the change (Boriah, 2010). Although time series approaches are highly recognized as a powerful class of techniques for change detection, their applicability for some problems is currently constrained by limitations of the underlying data. Specifically, small scale changes cannot be detected by these techniques and time series approaches are of limited value when the time series is of short length, such as when a satellite has just been launched (Boriah).

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Image acquisition

An essential aspect of change detection is selection of the appropriate satellite images. Recently with the development of earth observation systems, much variety of satellite data is now available, including satellite imagery acquired from sensors such as SPOT-HRVIR, Landsat TM or ETM, IRS-LISS and ASTER which have a spatial resolution from 5 to 30 m. New sensors (i.e. DMC) can acquire high resolution data (32 m) over a wide swath (600 km per orbit) which makes it well adapted for large-scale change detection (Congalton, 1996).

Species-Packing

One of the central problems in ecology is how the large number of species on Earth can coexist, and what sets limits on diversity. Hutchinson (1961) noticed that there were a large number of species of algae in lakes quite against the competitive exclusion principle, which suggests that in homogeneous and equilibrial systems, the number of coexisting species cannot exceed the number of resources. However, species may compete for a common resource, without being limited simply by its availability, because they differ in the way they utilize the resource. Space, in a variety of systems (e.g., forests, grasslands, coral reefs, and the marine benthic zones) is the direct object of competition among species and remains the ultimate limiting resource in such systems, yet, space may not be equally available to all species, and, also, individual species are limited not by the total amount of space, but in effect by the amount of space of a particular successional stage (time).

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The concepts of limiting similarity and species-packing (MacArthur & Levins, 1967) were harmonized by balancing processes that brought a suite of species together on an environmental gradient to be optimally packed. This subject has been widely studied (MacArthur, 1970; Abrams, 1983; Pacala & Tilman, 1994; Leibold, 1998; Kinzig, Levin, Dushoff, & Pacala, 1999; Chesson, 2000). In a related literature involving the effect of predators (or parasites, diseases, herbivores) on the process of competition, predatory pressure may play a regulatory role to stabilize competition. This concept is almost indubitable from observations of Darwin et al. (1998), to comments of Hutchinson (1948), to the keystone predator effect (Paine, 1974), to extensive experiments with herbivores in grasslands (Ryerson & Parmenter, 2001; Bakker & Olff, 2003), to the "Janzen/Connell hypothesis" (Janzen, 1970; Connell, 1978; Cordeiro & Howe, 2003) to more recent work with more complicated food webs (Spiller & Schoener, 1990; deRoos, McCauley, & Wilson., 1991; 1998; Vandermeer & Pascual, 2006) and the implied top down effect of predators on a lower trophic level. This has also been tested mathematically (Parrish & Saila, 1970; Cramer & May, 1972; Roughgarden & Feldman, 1975; Fujii, 1977; Hutson & Vickers, 1983; Kirlinger, 1986; Hofbauer & Sigmund, 1989).

Herbivore assembly rules and coexistence theories

For a proper insight into the ecological assembly rules of natural communities at a local scale, ecologists and conservation biologists have studied the mechanisms regulating and maintaining the species richness of animals (Lotka, 1925; Voltera, 1926; Gause, 1934; Pianka, 1966; Schoener, 1974; 1984;

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Drake, 1991; Tokeshi, 1999; Shurin & Allen, 2001; Cumming & Cumming, 2003). These studies resulted from the curiosity to know how sympatric species of living organisms manage to co-exist. It is expected that, as so many species share the same natural pastures, there will be overwhelming competition for their common food resource. Ecologists (e.g. Hutchinson, 1959; MacArthur, 1965; Pianka; Begon, Harper, & Townsend, 1996; Prins & Olff, 1998; Voeten, 1999; Brown, Fox, & Kelt, 2000; James & Shine, 2000) have often wondered whether there is no competition among herbivores living in the same area. This seemingly simple question has proved difficult to answer, despite the application of sophisticated experimental and mathematical approaches (e.g. Lotka; Voltera; Hutchinson, & MacArthur, 1959; MacArthur & Levins, 1967; Currie, 1991; Cornell & Karlson, 1997; Farnsworth & Beecham, 1999).

The theory of limiting similarities

The principle of limiting similarities introduced by MacArthur & Levins (1967), developed further by several other authors (MacArthur, 1970; May, 1974; Abrams, 1975, Prins & Olff, 1998) offered a sound scientific explanation for the factors determining coexistence. According to the principle of limiting similarity, coexistence of species within a guild is possible so long as species are not too similar. Implications here are that there is a limit to how similar species can be and still coexist. This theory proposes that different (sized) animals feed upon different food resources and thus, similar species will compete for food when niche overlap occurs. If the carrying capacity of the habitat is not

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high enough, competition between same-sized species continues until a single species occupies the habitat alone (MacArthur & Levins).

Furthermore, MacArthur and Levins (1967) concluded that the diversity of coexisting species could be limited in at least three ways depending on the circumstances. First, there is a lower limit to the abundance of each species, which sets the upper limit to the number of species. Second, there may be an upper limit to the abundance of each species set by the dangers of predators and diseases. Third, environmental instability sets a limit to the degree of specialization, and for a given degree of specialization, competition may, but does not always, set a limit to the similarity of coexisting species (MacArthur & Levins). The underlying information from this theory is that if species are too similar in many respects, in particular feeding habits, coexistence may not be possible when food resources are limited.

The Hutchinson's rule and body size

Hutchinson (1959) claimed that in both vertebrates and invertebrates, character displacement among sympatric species leads to sequences in which their body or appendage lengths often differ by a ratio of about 1.3, known as Hutchinson's rule. Since body weight scales to the power of around 2.5 – 3.0 to the length this ratio translates to a mean ratio of 2.0 in body weight (Case, Faaborg, & Sidell, 1983; Eadie, Broekhoven, & Colgan, 1987). Many workers applauded and recognized the 1.3 or 2.0 ratio as a biological constant (Schoener, 1984), while others dismissed the constant ratio rule, arguing that it was not based on sound scientific principle (Simberloff & Boecklen, 1981). Subsequently, a

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number of authors working with different taxa (e.g. fish (Brown, 1975), wandering spiders (Uetz, 1977), lizards (Schoener, 1970), birds (Schoener, 1974; Brown, 1975), bats (Macnab, 1971; Fleming, Hooper, & Wilson, 1972) and mammals (Brown, 1973; 1975)) reported constancy in ratio of sizes of adjacent species in a size ordered assemblage of various communities.

Based on Hutchinson's rule, the understanding is that competition is reduced primarily through differences in body size and secondarily through adaptations in trophic morphology, leading to differential preferences for grass height and forage quality (Bell, 1970; Jarman, 1974; Demment & van Soest, 1985; Owen-Smith, 1985; Illius & Gordon, 1987; Prins & Olff, 1998). Large herbivores have the ability to utilize high food biomass that is low in quality, but can tolerate low food biomass levels (Bell, 1971; Jarman; Demment, & van Soest; Illius & Gordon, 1987). Small species may thus benefit from the grazing impacts of larger species, and potentially out-compete the latter when food supplies become reduced (Illius & Gordon; Gordon & Illius, 1989; Prins & Olff). The body mass ratio determines whether facilitation or competitive displacement will occur within a given guild of grazers. Based on Hutchinson's rule, Prins and Olff hypothesized that in functional group, facilitation is more likely to occur at a weight ratio (WR) > 2.0, competition at WR < 2.0, while coexistence will occur at a WR = 2. Prins and Olff further hypothesized that when species are too similar in body mass, they might not profit sufficiently from facilitation interactions, and competition will occur. On the other hand when species are too different in body mass the larger herbivore will keep the grass at an equilibrium at which the

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vegetation quality is too low for small herbivores. In this case facilitation will not occur. Implications here are that there should be an optimal body mass difference, reflected by a constant body mass ratio between species of adjacent size. Although the size ratio was widely celebrated in the late fifties to seventies (Hutchinson, 1950; MacArthur & Levins, 1967; MacArthur, 1972; May, 1973), its validity as an ecological constant came under criticism in the early eighties (Nudds, Abraham, Ankney, & Tebbel, 1981; Simberloff & Boecklen, 1981; Eadie et al., 1987; Losos, Maeem, & Colwell, 1989). Simberloff and Boecklen in particular took issue with the lack of statistical analysis on data sets from which constancy in size ratios were claimed, arguing that most of those data sets were incomplete to qualify for any statistical analysis. Of 21 data sets claimed to conform to the 1.3 weight ratio, Simberloff and Boecklen reported that only seven were statistically significant at the 5% level and about half were significant at 30% level. Subsequent to this analysis, Simberloff and Boecklen dismissed the Hutchinson's Rule claiming that it had outlived its usefulness to evolutionary ecologists, a conclusion aggressively challenged by Schoener (1984), who argued that the tests used by Simberloff and Boecklen assumed biological unrealistic uniform distribution of body sizes. Schoener argued that statistical significance is hard to achieve no matter how narrowly defined taxonomically a group is if the number of species are small. Later, Eadie et al. (1987) argued that size ratios are a property of a wide variety of both animate and inanimate objects in nature and informs little about processes structuring animal communities. Despite these criticisms, the body weight ratio concept is among the most promising and

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interesting concepts for furthering understanding of interspecific herbivore-herbivore interactions, even though it is by no means clear yet at which level of relative abundance, coexistence, facilitation and competition may occur. In many herbivore communities, coexistence has been observed among ecologically similar species, especially grazers. Several ecological studies concluded that ecologically similar species manage to co-exist because of resource partitioning (Sinclair & Norton-Griffiths, 1982; Duncan, Foose, Gordon, Gakahu, & Lloyd, 1990; Fritz, De Garine-Wichatitsky, & Letessier, 1996; Tokeshi, 1999). Resources partitioning refers to the differential use of resources such as food and space, resulting in reduced resource use overlaps (Begon et al., 1996; Tokeshi). Prins and Olff argued that herbivore species of similar body weight could co-exist because of grass being a complex continuous food resource that is further modified by the grazing process.

Competition and facilitation

Competition is considered to be that major driving force causing differential resource utilization, although factors like predation and different responses to environmental gradients may also lead to resource partitioning (MacArthur & Levin, 1967; Crawley, 1983; Seifert, 1984; Prins & Olff, 1998; Tokeshi, 1999). According to the theory of resource competition, similar species can co-exist provided the food which each harvests most efficiently is different. Competition may arise where one species reduces shared food resources below the level that can be exploited efficiently by another species (Illius & Gordon, 1987; Prins & Olff). Alternatively, by reducing grass biomass one species may

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benefitanother by facilitation access to forage of a suitable height or quality (Vesey-Fitzgerald, 1960; Bell, 1970; 1971; McNaughton, 1976). The relative importance of these two processes in structuring species assemblages remains unclear. Species that exist without competition are said to be ecologically separated from others (Eltringham, 1979). Lamprey (1963) pointed out that ecological separation occurs through (i) the occupation of different habitat types, (ii) through the selection of different types of food, (iii) occupation of different areas in the same season, (iv) occupation of the same area in different seasons, (v) feeding at different levels in the vegetation, (vi) and occupation of different dry season refuges. All these mechanisms result in consumption of different food items, and it is usually through this differential food selection that competition is avoided.

Vegetation biomass productivity

Biomass productivity of vegetation also plays a significant role in interactions of herbivores. The optimal body mass difference for a given habitat is likely to depend on primary productivity, vegetation biomass-quality relationships and environmental fluctuations. When vegetation is at high biomass, only large herbivore species are able to maintain high consumption rates. If the density of large herbivores increases however, grazing pressure is increased, and as a result plant standing crop decreases. This in turn increases the growth rate of small herbivores. Hence at high biomass, large herbivores facilitate for small herbivores. When vegetation biomass is low, competition becomes more important. At low biomass the small herbivores keep vegetation at equilibrium, at

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very low levels where larger herbivores may not even be able to exist. Under this circumstance, competitive exclusion may occur (Prins & Olff, 1998). Under fluctuating conditions (e.g. annual variation in rainfall) the competition balance might vary between years, thereby allowing co-existence (Prins & Olff).

Herbivore Nutritional Ecology

Digestive strategies

Nutrition affects most aspects of herbivore ecology such as individual growth rates (Parker, Barboza, & Gillingham, 2009), the timing and success of reproductive efforts (Adamczewski, Flood, & Gunn, 1997), and vulnerability to predation (Mech, Smith, Murphy, & MacNulty, 2001) and diseases (Enk, Picton, & Williams, 2001). Ungulates feed on plant materials, consisting of soluble cell contents (Van Soest, 1996) surrounded by lignified cell walls that cannot be digested by vertebrate enzymes (Hume, 2002); and so fermentation by symbiotic bacteria is required (Iason & Van Wieren, 1999). Mammalian herbivores are classified into hindgut and foregut fermenters based on the fermentation site (Hume). Small-bodied caecal hindgut fermenters, such as rodents and lagomorphs, compensate for low digestive efficiency by practicing coprophagy (Van Soest), which prevents the loss of microbial protein through the faeces (Iason & Van Wieren). Larger, colonic hindgut fermenters, such as equids and elephantids, are adapted to digest large volumes of low quality forage (Duncan et al, 1990). They can increase their performance rate to cope with periods of low forage quality (Beekman & Prins, 1989) but are vulnerable when forage quantity is restricted (Janis, 1976). The majority of medium-sized herbivores are foregut

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fermenters (Duncan et al., 1990), and of these, most are ruminants (Dehority, 2002) that have large, sac-like fore-stomachs adapted for maximal forage digestion (Hume). Through repeated mastication (Fritz et al., 2009) and the prolonged retention of cell walls, ruminants significantly reduce ingesta particle size (Janis), and this maximises energy extraction, but can limit intake rate by restricting processing speed (Van Soest) and constraining feeding time (Duncan et al.), effects that are exacerbated by low forage quality (Janis). Ruminants are therefore more susceptible than hindgut fermenters to limitations imposed by quality (Illius & Gordon, 1992) but are better adapted to systems that experience periods of reduced forage quantity, although these can be problematic when feeding time is also constrained (Duncan et al.).

Diet type

Herbivore species vary in their proportional ingestion of grass and browse (Hofmann, 1989; Van Soest, 1996; Gagnon & Chew, 2000): diets range across the full spectrum of grass and browse composition (Codron et al., 2007), and seasonal variation in diet is not uncommon (Iason & Van Wieren, 1999; Ego, Mbuvi, & Kibet, 2003). Ungulates display various morphological features adapted to the botanical composition of their diets (Spencer, 1995), such as differences in the relative sizes of some alimentary tract organs (Hofmann, 1989), tooth crown height (Codron et al.), incisor arcade structure (Gordon & Illius, 1988) and muzzle width (Janis & Ehrhardt, 1988). The majority of these adaptations are related to differences in diet quality and distribution (Jarman, 1974; Gordon & Illius, 1994). Grasses contain higher proportions of cell walls and lower

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proportions of cell contents than browse leaves (Gordon & Illius, 1996), but lignin content is greater in the stems (Demment & Van Soest, 1985) and cell walls of browse species (Iason & Van Wieren), many of which have adaptations to deter herbivores (Laca, Shipley, & Reid 2001). These include chemical defences, such as high concentrations of tannins (Cooper, Owen-Smith, & Bryant, 1988), and physical defences, such as sharp spines (Cooper & Owen-Smith, 1986). Browsers therefore need to be highly selective in their feeding habits, using prehensile lips to avoid thorns (Hofmann, 1989) and ingesting only small portions of plants, such as small leaves at the ends of lignified stems (Van Soest). Grazers can afford to be less selective because the difference in quality within a grass plant is less extreme (Jarman, 1974) and the distribution of grass across the landscape is more uniform than that of browse (Spencer).

Nutritional allometry

Herbivore nutritional ecology is linked to body size (Illius & Gordon, 1992): ungulate gut capacity increases linearly with body mass (Demment & Van Soest, 1985), whilst energetic requirements scale with the three-quarter power of body mass (Van Soest, 1996), resulting in allometric feeding strategies (Illius & Gordon, 1987). Microbial fermentation is a slow process (Iason & Van Wieren, 1999), so the time required to digest cell walls can impose a constraint on energetic uptake (Hume, 2002). Large-bodied animals can process large quantities of low quality forage (Codron et al., 2007), whereas small-bodied animals must meet comparatively larger energetic demands (Demment & Van Soest) by feeding selectively on smaller quantities of high quality forage (Janis, 1976). Larger

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animals can therefore exploit a greater variety of habitat types (Du Toit & Owen-Smith, 1989), resulting in a more widespread distribution (Cromsigt, Prins, & Olff, 2009). Body size also affects the scale at which animals respond to forage heterogeneity (Du Toit & Cumming, 1999). Small animals increase their selectivity when resources are finely interspersed, whereas large-bodied herbivores feed indiscriminately on such patches (Laca et al., 2010). These allometric feeding strategies are also evident within species: between sexually dimorphic adults (Kirby, Shannon, Page, & Slotow, 2008) and between age classes with different body sizes (Van Soest).

Herbivore Spatial Ecology

Foraging theory

Herbivores feed on resources that are spatially static (Owen-Smith, Fryxell, & Merrill, 2010) but highly variable in their physical and nutritional characteristics (Hopcraft, Anderson, Perez-Vila, Mayemba, & Olff, 2012). The availability and quality of forage is affected by mechanisms inherent in the plant, such as growth and senescence, but also by external effects such as disturbance (Diaz et al., 2007). The amount of energy that a herbivore can gain from a feeding patch diminishes as forage is depleted (Owen-Smith & Novellie, 1982); the animal moves on to another feeding site when a certain threshold is reached (Stephens & Krebs, 1986). While animals must make maximum use of limiting resources they must also reduce the costs such as predation and energy spent through travel (Pyke et al., 1977). The costs and benefits of different behaviours

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depend on the condition and state of the animal (Owen-Smith et al., 2010): individuals suffering from poor nutrition will take greater risks when foraging than those in good condition (McNamara & Houston, 1987; Sinclair & Arcese, 1995). Landscapes are heterogeneous on several spatial scales: habitats of disparate value (Jones, Pilkington, & Crawley, 2006) occur in patches of differing size (Ahlqvist & Shortridge, 2010), whilst forage characteristics vary within habitat types (Augustine, 2003; Matson, Goldizen, Jarman, & McCorquodale, 2005). Herbivore foraging patterns are therefore subject to scale-dependent effects (Bailey et al., 1996): large-scale selection of a particular area restricts the availability of resources on which to base smaller-scale decisions (Senft et al., 1987). Herbivores must match their distribution to that of optimal resources (Senft et al.) to maximise their fitness (Bailey et al.). The rank order of the most profitable habitats varies temporally through disparate responses to climatic effects (Zweifel-Schielly, Kreuzer, Ewald, & Suter, 2009) caused by differences in soil type and nutrient content (Mbatha & Ward, 2006), resulting in seasonal fluctuations in herbivore space use (Holdo, Holt, & Fryxell, 2009).

Predation

Predation pressure is not equal for all herbivore species (Mills et al., 1995; Hopcraft et al., 2010); body size is an important factor (Cohen et al., 1993) determining the range of potential predators (Sinclair et al., 2003). Most predators prefer particular prey species (Owen-Smith & Mills, 2008), but small ungulates are more vulnerable than large-bodied herbivores because they are easier to capture and kill (Hopcraft et al.). This also applies within species: small young are

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more vulnerable than large adults (Linnell, Aanes, & Andersen, 1995), leading protective mothers to alter their spatial patterns to minimise predation risk to their offspring (Kie, 1999; Gaillard et al., 2010). In sexually dimorphic social species, this can cause differential habitat use by herds of breeding females and larger males (Hay, Cross, & Funston, 2008). The small groups formed by the latter can experience greater predation rates (Owen-Smith, 2008), resulting in sexually disparate mortality rates (Creel, Winnie, Maxwell, Hamlin, & Creel, 2005). Predation can play a large role in herbivore population regulation (Grange et al., 2004; Ogutu & Owen-Smith, 2005), and can influence social structure (Fryxell, 1991; Kie, 1999), vigilance behaviour (Underwood, 1982) and distribution (Russell, Swihart, & Feng, 2003) at several spatial scales (Valeix et al., 2009). The predation risk factor is therefore important in herbivore spatial ecology (Hebblewhite, Merrill, & McDonald, 2005; Willems & Hill, 2009), illiciting caution on the landscape (Laundré, Hernandez, & Altendorf, 2001) that ungulates must consider during habitat selection (Gaillard et al., 2010). The effect of perceived predation risk varies with herbivore characteristics (Smit, 2011; Hopcraft et al., 2012), but also with the density (Hebblewhite et al.), diversity (Lima, 1992) and species of carnivores (Willems & Hill). In systems dominated by coursing predators, herbivores favour wooded habitats where predation risk is lower (Creel et al., 2005). In areas where the dominant carnivore is an ambush hunter (Hopcraft, Sinclair, & Packer, 2005), potential prey species select open habitats (Massé & Côté, 2009) that offer greater visibility and therefore more effective predator detection (Hay et al., 2008), and more space in which to flee

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from attack (Ripple & Beschta, 2004). Predation pressure could also be one of the drivers of large-scale movements (Hebblewhite & Merrill, 2009). Migratory species frequently experience lower predation rates than resident ones (Hebblewhite & Merrill, 2007; Anderson, Hopcraft, Eby, Ritchie, Grace, & Olff, 2010) by avoiding areas used by territorial carnivores (Fryxell & Sinclair, 1988).

Anthropogenic factors

Migratory herbivores need access to large areas (Bartlam-Brooks, Bonyongo, & Harris, 2011) across which to track resource gradients (Holdo et al., 2009). These spatial requirements are under increasing threat from anthropogenic interference: increases in resource extraction plants (Berger, 2004), roads and fences (Holdo, Fryxell, Sinclair, Dobson, & Holt, 2011) have disrupted large scale movements. This can decrease carrying capacity (Ben-Shahar, 1993) and even cause widespread death by preventing access to critical resources (Spinage, 1992). Increased effects of habitat loss and poaching have reduced the populations of migratory terrestrial mammals across the world (Harris, Thirgood, Hopcraft, Cromsigt, & Berger, 2009), but resident populations are also declining, even in PAs (Craigie, Baillie, Balmford, Carbone, Collen, Green, & Hutton, 2010). Outside PAs, intensive livestock grazing can change the composition (Otuoma, Kinyamario, Ekaya, Kshatriya, & Nyabenge, 2009) and quality of habitats available to wildlife (Mamo & Bekele, 2011), whilst expanding human settlements restrict the range of herbivore species (Ogutu et al., 2010) and can prevent access to limiting resources (Mamo & Bekele). Habitat fragmentation reduces the capacity for gene flow between populations by preventing dispersal

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(Heller, Okello, & Siegismund, 2010) and causes herbivores to occupy small pockets of space, where they are more vulnerable to hunting (Cullen, Bodmer, & Padua, 2000). Bushmeat poaching, which, in Africa, focuses on large-bodied ungulate species inside and outside of PAs (Fa, Ryan, & Bell, 2005), can cause marked changes in the composition of the herbivore community (Laurance et al., 2006). Poaching pressure can alter the activity patterns of hunted species through increased nocturnal activity (Di Bitetti, Paviolo, Ferrari, De Angelo, & Di Blanco, 2008), a higher tendency for flight (Caro, 1999), greater vigilance (Averbeck, Apio, Plath, & Wronski, 2010) and smaller herds (Fischer & Linsenmair, 2007), all of which can affect population dynamics (Manor & Saltz, 2003) and increase predation risk (Kilgo, Labisky, & Fritzen, 1998). Herbivores suffering from high hunting pressure often avoid areas close to human access points, such as roads (Laurance et al., 2006; Webb, Dzialak, Harju, Hayden-Wing, & Winstead, 2011), although areas with relatively high levels of anthropogenic disturbance can be attractive to some species through reduced predation risk (Hebblewhite & Merrill, 2009), or access to limiting nutrients. However, when these are associated with habitats close to roads, herbivores can experience higher mortality rates (Laurian et al., 2008). Anthropogenically-induced climate change has the potential to influence many aspects of herbivore ecology through alterations in the growth patterns (Rivrud, Loe, & Mysterud, 2010), distribution, and relative abundances of plant species (Wang, Hobbs, Singer, Ojima, & Lubow, 2002), caused by their differential responses to changes in rainfall patterns and temperature (Peinetti, Kalkhan, & Coughenour, 2002). Continued selection for optimal habitats could

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change the distribution of herbivores (Luzhang et al.., 2005) through geographical shifts in species' ranges (Hu & Jiang, 2011) that could reduce the future conservation value of PAs defined according to current herbivore populations and spatial requirements (Singh & Milner-Gulland, 2011). Changes in forage availability could affect the sizes of herbivore home ranges (Rivrud et al, 2010) and impact their population dynamics, possibly intensifying density-dependent effects (Wang et al., 2002). The responses of regional ecosystems to climate change are difficult to predict (Colchero, Medellin, Clark, Lee, & Katul, 2009), particularly tropical systems that are driven by water rather than temperature (Midgley & Thuiller, 2011). The structure and functioning of those ecosystems are likely to change substantially (Romme & Turner, 1991), with the potential for both increases (Wang et al., 2002) and decreases in the populations of particular herbivore species (Hu & Jiang, 2011).

Protected Areas (PAs)

Conservation is defined as the management of human use of the biosphere so that it may yield the greatest sustainable benefit to present generations, while maintaining its potential to meet the needs and aspirations of future generations (International Union of Conservation of Nature, flora and fauna (IUCN), 1994). Biodiversity refers to the variability among biological organisms from all sources, including terrestrial, marine and other aquatic ecosystems, and the ecological complexes of which they are part. It includes diversity within species (genetic diversity), between species and of ecosystems.

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Conservation of biodiversity in Protected Areas (PAs) therefore seeks to preserve ecosystems and natural habitats and to maintain and recover viable populations of species in their natural surroundings and, in the case of domesticated or cultivated species, in the surroundings where they have developed their distinctive properties.

By ensuring the protection of natural habitats to the extent that the integrity of all of its ecological functions are maintained, this PA approach has been demonstrated to be the best opportunity to ensure the fullest possible protection of biodiversity in the Savanna landscapes of Africa. Biodiversity conservation in the PAs is also a vital contribution to the conservation of the world's natural and cultural resources. Its value ranges from the protection of natural habitats to associated flora and fauna, against destruction and extinction respectively, to the maintenance of both the environmental services of the respective ecosystems as well as the maintenance of the environmental stability of the surrounding regions. The success of conservation also requires a modification of how we value economic goods and services in the short, medium and long term (Mcneely, 1992).

In Africa PAs occupy slightly over 2 million sq. km or 7 % of the continent's 30 million sq. km (IUCN, 1994). Unfortunately, these PAs are poorly distributed and lack adequate policies for their management in a network framework. Many unique and fragile drier ecosystems in northern Africa, for example, are yet to be adequately protected (IUCN). The opportunity for pro-active measures to conserve biodiversity in most of Africa thus is still very high.

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It is on this basis that many African countries are now on the rush to develop systems of PAs based on the six categories defined by the IUCN guidelines for PAs management categories as Strict Nature Reserve, Wilderness Area, National Park, Natural Monument, Habitat / Species Management Area or Protected Landscape.

PAs such as nature reserves have been found to be effective in preventing habitat destruction and protecting ecosystems within their borders. PAs are the cornerstones of conservation strategies worldwide. They preserve key ecosystems against biodiversity loss (Myers, Mittermeier, Mittermeier, Da Fonseca, & Kent, 2000), promote sustainable management and offer unique laboratories to investigate ecosystem functioning and complexity. Virtually all major managerial problems facing PAs today have a human component. Within Africa, the commonest of these relate to the increasing human settlement of adjacent lands and the unauthorized harvesting of resources within the PAs. As human populations increase and the demand for resources grows, the frequency and intensity of conflict between PAs and local people will increase (Newmark, Manyanza, Gamassa, & Sariko, 1994).

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CHAPTER THREE: MATERIALS AND METHODS

Study Area

The Mole National Park (Figure 1) covers an area of about 4,840 km^2 as Ghana's largest wildlife refuge. The Park is located in northwest Ghana on grassland savanna and riparian ecosystems, with a sharp escarpment forming the southern boundary of the Park. The Park's entrance is reached through the nearby town of Larabanga, some 15 km from Damongo, the capital of Gonja District. The Lovi and Mole Rivers are ephemeral rivers flowing through the Park, leaving behind a few drinking holes during the long dry season. This area of Ghana receives an average of 1,100 mm per year of rainfall (Wildlife Division, 2011). In the 1930s the British Colonial Administration designated some 2,300 km^2 of the present park as a Game Clearance Area in an effort to control tsetse flies. The aim was to clear the area of wildlife and large numbers of antelope and buffalo were shot but fortunately the policy of game clearance was abandoned in 1957. In 1958 Mole Game Reserve was established, enclosing some traditional hunting grounds and sacred sites. The park was re-designated a National Park in 1971 after the small human population of the area was relocated.

Tree species of the Park include *Burkea africana* Hook., *Isoberlinia doka* Craib.& Stapf., *Vitelleria paradoxa* C.F.Gaertn., *Detarium microcarpum* Guill. & Perr., *Anogeissus* sp. A. J. Scott, and *Terminalia macroptera* Guill. & Perr. There are few main habitat types including riverine, swamp, closed savanna woodland and open savanna woodland but the open savanna woodland is the dominant habitat type (Schmitt & Adu-Nsiah, 1993). The savanna grasses are somewhat

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low in diversity but known species include sedges, *Kyllinga echinata* S. S. Hooper., *Aneilema setiferum* A. Chev., and two endemic members of the Asclepiadaceae subfamily, the vine *Gongronema obscurum* Bullock., and the edible geophyte, *Raphionacme vignei* E. A. Bruce.

The Park is home to over 93 mammal species, and the large mammals of the Park include the savanna elephant (*Loxodonta africana africana* Blumenbach, 1797), hippopotamus (*Hippopotamus amphibious* Linnaeus, 1758), buffalo (*Syncerus caffer* Sparrman, 1774, and warthog (*Phacochoerus aethiopicus* Pallas, 1766) The Park is considered a primary African preserve for antelope species including kob (*Kobus kob* Erxleben, 1777), Defassa waterbuck (*Kobus defassa* Rüppell, 1835), roan (*Hippotragus equinus* Desmarest, 1804), hartebeest (*Alcelaphus bucelaphus* Pallas, 1766), oribi (*Ourebia ourebi* Zimmermann, 1783), bushbuck (*Tragelaphus scriptus* Pallas, 1766), and the yellow-backed duiker (*Cephalophus sylvicutor* Afzelius, 1815). Various species of primates including olive baboons (*Papio anubis* Lesson, 1827) and black-and-white colobus (*Colobus polykomos* Zimmermann, 1780), which are heavily represented. Sightings of hyaenas (*Crocuta crocuta*, Erxleben, 1777), lions (*Panthera leo* Linnaeus, 1758) and leopards (*Panthera pardus* Linnaeus, 1758) are now unusual, but these carnivores were once very common in the Park. However, current trends in raids by hyenas in the communities call for investigation of their population. Thirty-three species of reptiles (Leaché, 2005) and 344 bird species (Lemaire-Dowsett & Dowsett, 2005) have been listed for MNP. The remnant human population of the Park was removed in 1961, leaving all game hunters outside of

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the reserve, meaning that mammal populations at the edges of the Park are more heavily affected by hunting than interior populations. The Park shares borders with four districts and 33 communities with a total population of about 40,000 people. Human-wildlife conflicts, which result from raids of crops and livestock in the communities by the protected animals, have been reported more frequently of late, with elephants, hyaenas and baboons being the worst offenders. On the other hand, many people in the fringe communities poach wild animals from the Park and as a result have sometimes deadly encounters with the Park's field staff. MNP experiences four seasonal events every year (Table 1).

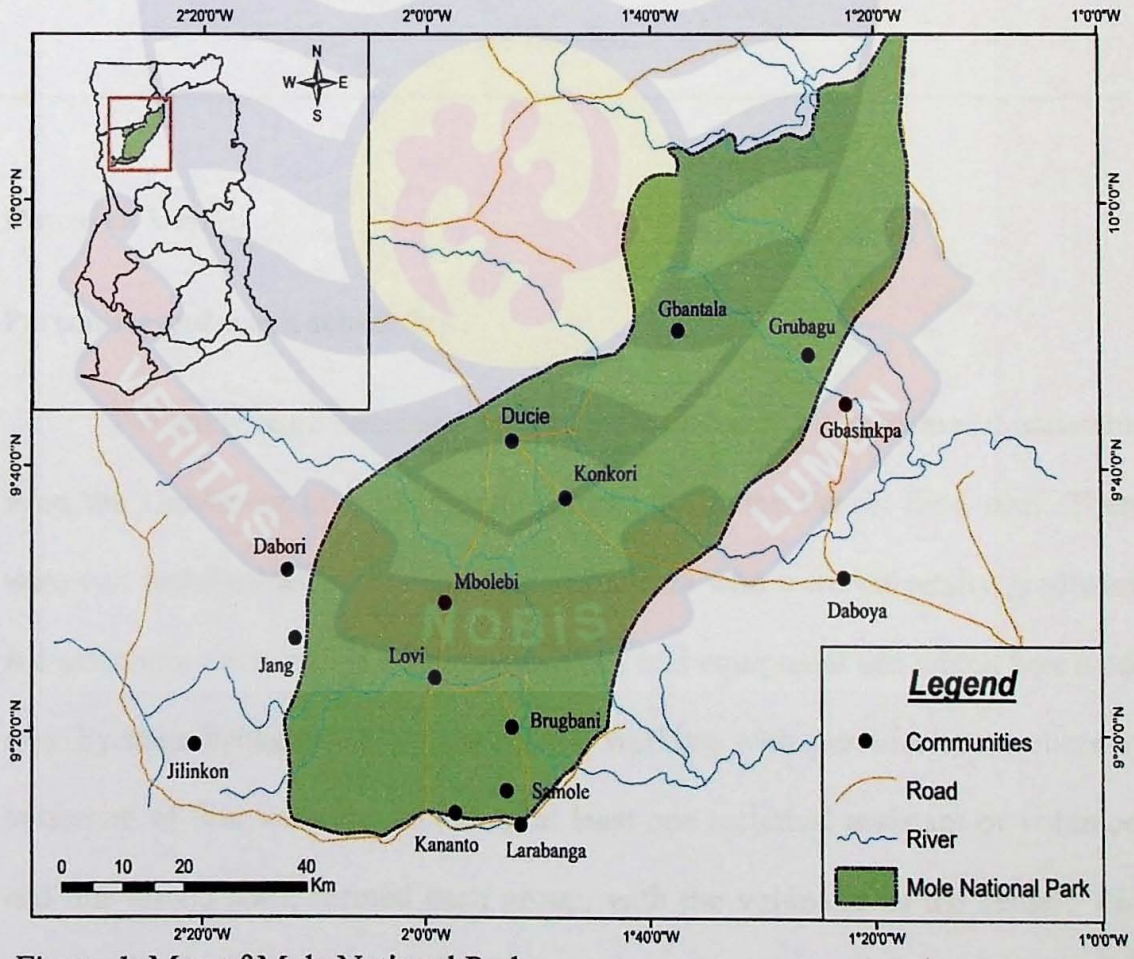


Figure 1: Map of Mole National Park.

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Table 1

Different Seasons at Mole National Park

Season	Description	Period
Dry	Harmattan with low humidity	October - December
Fire	Dry harmattan with low humidity; windy	January - April
Rainy	Heavy rains with lightening and thunder	May - July
Flood	Slight rains; Lowlands are flooded.	August - September

Research Design

Personnel and work schedule

The study team consisted of workers who were either technical assistants from the University of Cape Coast, volunteers, or the Park's field staff. There were two technical assistants and four volunteers who were university graduates. All assistants were trained on the procedures and equipment use which was made easy by their backgrounds or experience working with previous researchers. A minimum of four workers, including at least one technical assistant or volunteer and one armed staff, formed each group, with the volunteer as the leader. Two

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groups were based in each study block, though they were sometimes deployed to other blocks to assist other groups from time to time.

Each group located places for ground truth assessment following GPS co-ordinates picked from satellite imagery and also demarcated transects for mammal surveys. Ground truth assessment was used to obtain accurate ground locational point data of land cover classes, to validate the land cover class data included in the classification scheme of satellite imageries. As some of the places that were assessed for ground truth were also used as point transects, the two activities were undertaken simultaneously in August–September, 2013 until all transects were demarcated. Ground truth assessment continued to December, 2013.

Long transects that could not be driven required 2-4 groups to survey in a day and so it was necessary to deploy groups from other blocks to support. Such transects were divided into 2-4 parts and surveyed by walking. The schedules were planned so that each block could be worked at least twice a month and also reduce the cost of hiring vehicles. Surveys were conducted in the morning and evening for a continuous period of 10 days every month. All the 20 point transects were surveyed in a day in all the blocks, leaving nine days to survey line transects including time spent for commuting between blocks. Transects were surveyed from September, 2013 to August, 2014. Between September and December, 2013, two extra days were used to complete ground truth assessment.

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Ground truth accuracy assessment of land cover classes

Landsat refers to a series of satellites put into orbit around the earth to collect environmental data about the earth's surface (http://landsat.gsfc.nasa.gov/). Since 2003, a mechanical fault in the Scan-Line Corrector (SLC-Off) of the Landsat-7 satellite resulted in a 22–25% data loss in each image (Boriah, 2010).

Landsat satellite imagery (Landsat ETM + at 30-m spatial resolution) in unsupervised mode for 1980, 1985, 1990, 1995, 2000, 2005, 2010 and 2013 were acquired from the Forestry Commission, Ghana. The land cover classes obtained from classified images in the unsupervised mode by the remote sensing software were (i) closed savanna woodland, (ii) open savanna woodland, (iii) shrub/dense herbaceous, (iv) grass/herbaceous, and (v) bare/built-up area. Table 2 gives a description of these land cover classes. Specific factors were considered for data collection: (i) geographic distribution, an attempt to obtain point data evenly throughout the study area; (ii) proximity of routes, for travel logistic purposes; and (iii) comprehensive classification, to ensure that adequate point data were collected for all land cover classes obtained from the satellite imagery (Congalton, 1996). It was not practical to obtain an even coverage of ground truth data for the entire study area. An attempt was made during the field surveys to collect as many samples as possible, but this was logistically difficult for all land cover classes. Congalton states that collecting a minimum of 50 samples for use in an error matrix is a good rule of thumb. Fewer data points were envisaged for some of the land cover classes due to the difficulty of locating a plot of 200 m x 200 m for each class at various places in the Park for the assessment surveys. To

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compensate for this, smaller plots of 30 m x 30 m were randomly sampled and surveyed in each field site at six to nine different locations (Table 3) and every effort was made to collect additional data from 30 m x 30 m field sites for those classes. It was assumed that replicates in any field site were considered separate data points for scoring in the accuracy assessment.

Altogether 300 samples, 60 for each class (Table 3), were assessed for ground truth accuracy. Each field site was traced and located at 10 different places for open savanna and grass, seven different places for closed savanna and shrub/dense herbaceous, and six for bare/built-up. A 30 m x 30 m plot was surveyed randomly six times for each of open savanna and grass classes, seven times for closed savanna and shrub/dense herbaceous, and nine times for built-up. In addition, a 30 m x 30 m field site was traced and located for closed savanna at 11 places, shrubs (11 places) and bare/built-up (six places) (Table 3).

Transect setting

Table 4 gives the descriptions of the main habitat types in MNP, namely (1) the *Burkea-Terminalia* open savanna woodland with *Vitellaria paradoxa* (BTV), (2) the *Burkea-Terminalia* savanna woodland with *Detarium microcarpum* (BTD), (3) the *Anogeissus* with *Vitellaria paradoxa* (A), (4) the boval vegetation (*Loudetiopsis kerstingii-Polycarpaea tenuifolia* community on rocky substrates, (5) riverine forest (R) along most of the rivers in the park, and (6) swamp (Schmitt & Adu-Nsiah, 1993). The closed savanna woodland in the land cover classification scheme was made up of the riverine forest, mostly and the BTD, BTV and Anogeissus the open savanna class. In general, MNP shows a

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fine scale mosaic of habitats over a long transect, which was formed through an ecological disturbance, probably fire. A habitat mosaic is ecologically important in creating or maintaining biodiversity as it introduces variability in vegetation composition of habitats.

The Park was divided into three study sites (blocks) namely, North, Central and West (Figure 2). The Park is managed at range levels and, administratively, field staff are deployed from four ranges, namely Bawena, Dusie, Headquarters and Jang. In this study, much of the Dusie range was not studied due to accessibility and so study sites were not defined in terms of the existing administrative ranges. Instead, Bawena Range and part of Dusie Range at the northern part of the Park formed the North block. The Headquarters Range and part of Dusie formed the Central block, and the Jang Range and part of Dusie at the west of the Park formed the West block.

Strip transects of 200 m width each, 100 m at each side of the strip, and varying lengths were selected along existing roads and paths traversing the main habitat types in each study block. Point transects, each measuring 500 m x 500 m, were also demarcated in each habitat type of each block as there were not that many strips that could be driven. These points were demarcated by existing landmarks and dimensions mapped out by a range finder (Yardage Pro Compact 800, Bushnell Factory, Overland, KA, USA) to take the shape of a square from which the area could be calculated. Both strip and point transects were distributed to ensure as much spatial representation as possible in each block and their locations were then mapped by a GPS (all Garmin Ltd., Olathe, KA, USA). The

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length of each habitat type traversed by a transect was recorded using GPS and the area, width x length, of each transect was calculated. The area of each habitat within a strip transect was calculated by multiplying the length of each section of a particular habitat by the transect width and then summing all the areas of the same habitat in the transect.

There were 16 strip transects and 20 point transects. Four strip and eight point transects were in the North block, seven strip and five point transects in the Central block, and five strips and seven point transects in the West block. The total area occupied by all the transects was 75.88 km^2 (Table 5) which represented about 1.6% of the Park. Details of the habitat types in each transect are shown in Table 5.

Spatial data from the GPS were downloaded onto a computer. Data obtained in degree decimals were converted into database file and exported to ArcGIS (v9.3) to be projected in a Geographic Coordinate System. These coordinates were then plotted as individual points which were joined together to form the shapes of the transects (Figure 3).

As accessibility and logistics made it difficult to spread sampling effort over the entire Park, the actual surveyed study area was 63% of the 4,840 km^2 Park. This was estimated by laying square grids of equal area on the map of the Park using ArcGIS (v9.3). All the full-, half-, and quarter-grids, etc. outside the surveyed study area within the Park were added as 1, ½, ¼, etc. respectively, and the number obtained multiplied by the size of the grid to give the size of the study area that was not surveyed.

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Table 2

Description of Land Cover Classes

Land cover class	Description
Closed savanna woodland	Savanna vegetation dominated by woody plants, mostly trees, which are close to each other and often forming canopies that shade the vegetation floor from sunlight.
Open savanna woodland	Savanna vegetation with admixture of woody plants, mostly trees, and herbaceous plants. Trees dominating the vegetation somehow but are well spaced, forming few or no canopies and therefore admitting enough sunlight at the vegetation floor.
Shrub / dense herbaceous	Shrubs interspersed with a mixture of largely dense herbaceous plants with little wood and few dense herbaceous plants with no wood.
Grass / herbaceous	Mostly grasses interspersed with few other herbaceous plants.
Bare / built-up area	Bare area without vegetation, including water bodies, buildings, rocky surfaces and roads.

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Table 3

Sampling Details for Ground Truth Accuracy Assessment for each Class

	Classes				
Quadrats at field sites	Open savanna	Closed savanna	Shrub	Grass	Bare/ built-up
Number of 200 m x 200 m	10	7	7	10	6
(No. of replicates of plots at field site)	(6)	(7)	(7)	(6)	(9)
No. of additional 30 m x 30 m	-	11	11	-	6
Total no. of 30 m x 30 m sample plots	60	60	60	60	60

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Table 4

Descriptions of the Habitat Types in the Study Area

Habitat	Description
Anogeissus	Open savanna woodland found on granite outcrops. Dominant species is *Anogeissus* sp.
Boval	All plant communities on flat iron pans with patches of shallow soil. Mainly annuals when flooded and species-rich during the rains and subject to extreme water-stress during the dry season. Dominant species are *Loudetiopsis kerstingii* and *Polycarpaea tenuifolia*
BTD	Open savanna woodland confined to shallow and rocky soils. Dominant species are *Burkea* sp., *Terminalia* sp., with *Detarium microcarpum*
BTV	Open savanna woodland comprising all savanna woodland on well-drained and often deep soils. Dominant species are *Burkea* sp., *Terminalia* sp. with *Vitellaria paradoxa.*
Riverine	Found along most of the rivers. It often forms bands of generally dense and species-rich forests of up to 38m in height.
Swamp	Waterlogged areas, usually lowlands.

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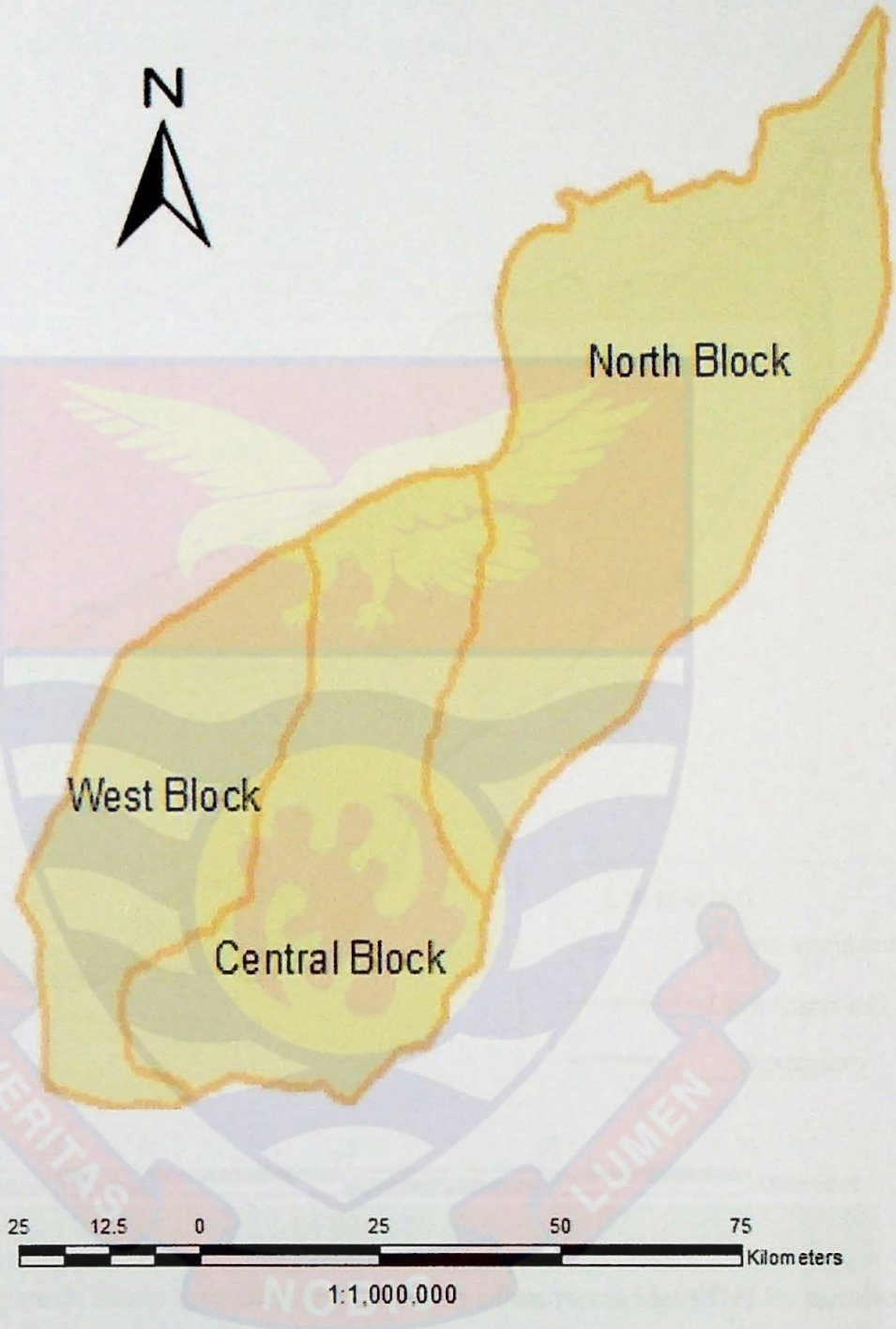


Figure 2: Study area showing study blocks.

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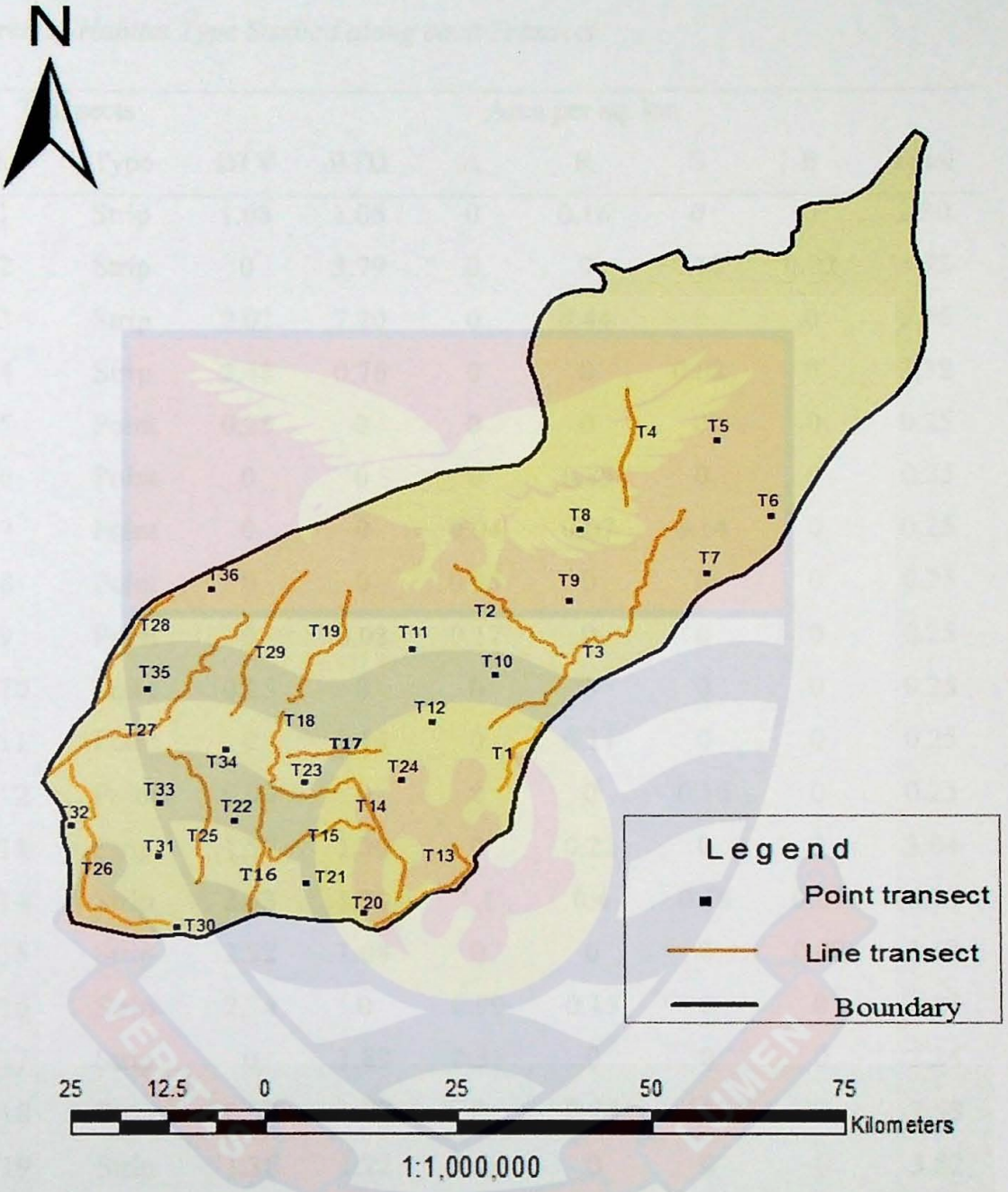


Figure 3: Study area showing locations of transects identified by numbers.

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Table 5

Area of Habitat Type Studied along each Transect

Transects		Area per sq. km						
Id.	Type	BTV	BTD	A	R	S	B	Total
T1	Strip	1.08	1.06	0	0.16	0	0	2.30
T2	Strip	0	3.79	0	0	0.11	0.02	3.92
T3	Strip	2.02	7.20	0	0.44	0	0	9.66
T4	Strip	2.48	0.76	0	0	0.08	0	3.32
T5	Point	0.25	0	0	0	0	0	0.25
T6	Point	0	0	0	0.25	0	0	0.25
T7	Point	0	0	0.04	0.07	0.14	0	0.25
T8	Point	0	0	0.25	0	0	0	0.25
T9	Point	0	0.08	0.17	0	0	0	0.25
T10	Point	0.25	0	0	0	0	0	0.25
T11	Point	0	0.14	0	0.11	0	0	0.25
T12	Point	0.09	0	0	0	0.16	0	0.25
T13	Strip	1.52	1.30	0	0.22	0	0	3.04
T14	Strip	2.33	1.30	1.1	0.4	0.58	0.03	5.74
T15	Strip	2.52	1.08	0	0	0	0.08	3.68
T16	Strip	2.74	0	0.99	0.15	0	0	3.88
T17	Strip	0	1.89	0.35	0	0	0	2.24
T18	Strip	0.57	1.77	0	0.24	0	0	2.58
T19	Strip	1.36	1.22	1.24	0	0	0	3.82
T20	Point	0	0	0.25	0	0	0	0.25
T21	Point	0.25	0	0	0	0	0	0.25
T22	Point	0	0	0.06	0.19	0	0	0.25
T23	Point	0	0.25	0	0	0	0	0.25

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Table 5, continued.

Transects		Area per sq. km						
Id.	Type	BTV	BTD	A	R	S	B	Total
T24	Point	0	0	0	0	0.25	0	0.25
T25	Strip	1.45	0	2.76	0	0	0.11	4.32
T26	Strip	2.78	1.88	1.8	0	0	0	6.46
T27	Strip	4.56	2.77	0	0.26	0	0.07	7.66
T28	Strip	2.5	1.2	0	0	0	0	3.7
T29	Strip	1.27	1.33	1.96	0	0	0	4.56
T30	Point	0.25	0	0	0	0	0	0.25
T31	Point	0	0	0	0.25	0	0	0.25
T32	Point	0	0	0	0.25	0	0	0.25
T33	Point	0	0.25	0	0	0	0	0.25
T34	Point	0	0	0.25	0	0	0	0.25
T35	Point	0.25	0	0	0	0	0	0.25
T36	Point	0	0	0.25	0	0	0	0.25

(Id. = identity, A = Anogeissus, R = Riverine, S = Swamp)

Equipment design and use

Quadrats, of area 1 m x 1 m were used to sample a plot within each habitat type of a strip or point transect to estimate percentage grass greenness (GG), percentage grass cover (GC) and grass biomass (GB) and obtain grass samples for chemical analyses to determine their percentage digestible organic matter (DOM) and percentage crude protein (CP). On each side of the quadrats, metre rules and metre-long cane sticks were nailed at 10 cm intervals. A quadrat was thrown to sample an open habitat or short grasses and a metre rule thrown to sample a closed habitat or tall grasses, in which case three other metre rules were joined to

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it to complete a quadrat. When necessary, twines were used to partition the quadrats and 100 squares were obtainable from each quadrat to get percentage estimates.

Various kinds of GPSs including two Garmin GPSMAP 62sc with inbuilt 5-megapixel autofocus digital camera, two Garmin eTrex GPS Receiver, one Garmin etrex Cx and three Garmin eTrex 10 Worldwide GPS Handled Navigator (all Garmin Ltd., Olathe, KA, USA) were used to record waypoints of transects, habitats, mammal species, locations, and the altitudes of habitats and where mammals were seen. For long transects, and sometimes habitats with tall grasses, a Garmin GPSMAP 62sc was used to save time as mammals were captured with the camera and each photo automatically geotagged with the location where it was taken. Two kinds of binoculars comprising four Bushnell 12 x 50 Permafocus and three Bushnell H_2O Proof Prism Binocular 10 x 42-mm were used (Bushnell Corp, Overland, KA, USA). Two laser range finders (Yardage Pro Compact 800, Bushnell factory, Overland, KA, USA) were used to measure distances from spots and guide the observer to the width limits of a transect in count surveys, otherwise groups relied on subjective judgement. Transect width was set to correspond to the distance at which a person walking perpendicular to the strip disappeared. Groups without a Garmin GPSMAP 62sc or a rangefinder were trained to estimate distances and bearings to mammals sighted and GPS positions on the transect were recorded. This made it possible to record the actual GPS positions where the mammals were sighted later by tracing the distance and bearing from the spot on the transect.

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Data Collection

Temperature and rainfall data were acquired for the MNP from 1980 to 2013 as well as Landsat satellite images of the MNP for the years, 1980, 1985, 1990, 1995, 2000, 2005, 2010 and 2013. Class values were declared by accuracy (ground truth) assessment on the field.

Large grazers, elephant, buffalo, roan antelope, waterbuck, hartebeest, kob, warthog and bushbuck were counted by driving or walking transects during their feeding times to estimate densities, biomass densities, and abundance and to determine their population trends. Grazers refer to species which use substantial amount of grass as forage. In this study, mammals the size of a bushbuck or larger, weighing at least 60 kg, were included as large grazers.

Grass related biotic factors, like grass quantity and quality, were measured. This was done by sampling plots using quadrats and metre-rules for grass samples to determine percentage grass greenness (GG) (Groom & Harris, 2010), percentage grass cover (GC) and grass biomass (GB). Radiographic analysis was used to determine percentage crude protein (CP) and percentage digestible organic matter (DOM).

Abiotic and anthropogenic factors like (i) nearest distance of mammals from boundaries, (ii) distance of mammals from nearest community or farm, (iii) distance of mammals from the nearest source of water, and (iv) altitudes by recording GPS readings at all mammal locations.

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Counting of mammals commenced from the start of a transect to the end while taking GPS readings of mammal locations and sampling plots for grass samples.

Acquisition of climate, land cover and vegetation data

Rainfall and temperature data from 1980 to 2013 (Appendix A) were acquired from the Bole-Bamboi District Meteorological Office, which monitors the rainfall and temperature patterns from their station at the Park's headquarters.

Field sites were demarcated using existing landmarks and dimensions mapped out using a rangefinder. The vegetation was surveyed to compare the classification in the supervised mode on the field with the one obtained in the unsupervised mode performed by the remote sensing software, to verify whether it was the same as its land cover class assigned by the remote sensing classified imagery. The number of times a class on the field was the same as the one obtained in the unsupervised mode was recorded. Also, the number of times a class on the field deviated was recorded.

Selectivity and overlap of habitat use by the grazers

Selection of the six habitat types by grazers was calculated using the selection index, E of Jacobs (1974), as described by Gordon (1989).

$$E = (U_i - A_i) / \{(U_i + A_i) - 2\,(U_i \times A_i)\} \quad (1)$$

where U_i is the proportion of sighting in habitat i and A_i is the proportion of the study area occupied by habitat i. E is defined as the relative difference between

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use and availability of a habitat type and gives an indication of relative feeding densities of animals on each habitat type. The value of *E* ranges from -1 to +1; values between -1 and 0 imply the species avoids the habitat type and values between 0 and +1 indicate selection of the habitat type (Gordon, 1989).

Habitat use overlap was calculated using Morisita's measure, C_λ of resources use overlap described by Horn (1966).

$$C_\lambda = 2 \Sigma (x_1 y_1) / (\lambda_x + \lambda_y)(XY), \quad \ldots\ldots (2)$$

where x_1 is the number of observations for species x; y_1 is the number of observations for species y; X is the total number of observations for species x; Y is the total number of observations for species y;

$$\lambda_x = \Sigma x_1 (x_1 - 1) / X (X - 1) \quad \text{and} \quad \lambda_y = \Sigma y_1 (y_1 - 1) / Y (Y - 1), \quad \ldots\ldots (3)$$

where λx and λy can be interpreted as the probability that two observations drawn randomly from populations X and Y both belong to the same category, relative to the probability of randomly drawing two observations of the same category from X and Y alone (Horn, 1966). Overlap between species x and y is absent when $C_\lambda = 0$ and complete when $C_\lambda = 1$. Morisita index was used following the recommendation by Henk (1981) to avoid the complex dealings with effects of sample size and diversity.

Mammal counts, densities and species-packing

The following assumptions were made (i) every large grazer that occurred on a transect was detected, (ii) all mammals were detected at their initial positions

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when first sighted, (iii) all targeted mammals were identified per every observation accurately, and (iv) mammal observations were independent of each other as one observation did not affect another.

At a speed of 20 km/hr, strip transects were driven (Figure 4) over a period of one year to collect data in the dry (Table 1, Figure 5), fire (Table 1, Figure 6), rainy (Table 1, Figure 7) and flood (Table 1, Figure 8) seasons. Mammals were viewed within the transect, with the help of binoculars when it was necessary, and counted between 07.30-10.30 GMT and 16.00-18.00 GMT. These were the feeding times of the mammals studied. Each strip or point transect was surveyed in one day and where necessary the survey of a strip was continued in the evening of the day as there is no significant difference between morning and evening counts (Groom & Harris, 2010). Surveys in the rainy and flood seasons were more difficult without a vehicle due to the tall grasses (Figure 9) and so it was sometimes necessary to divide strips to survey by walking a short strip to save time.

For each strip or point, all animals of a species within a specified habitat were counted. The results of a non-parametric Mann-Whitney comparability test by Groom and Harris (2010) indicated a not significant difference between strip and point count methods and so density estimates derived from the two methods were directly comparable.

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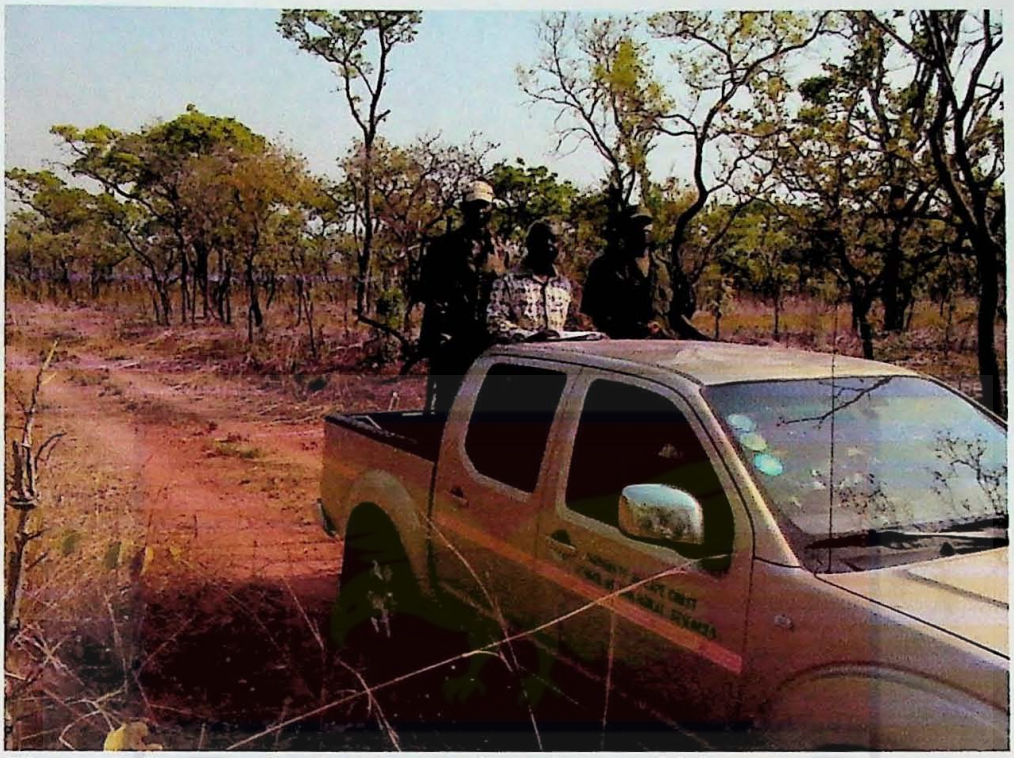


Figure 4: Survey of strip transects by using a vehicle.



Figure 5: Part of the Park in the dry season.

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Figure 6: Part of the Park in the fire season.



Figure 7: Part of the Park in the rainy season.

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Figure 8: Part of the Park in the flood season.



Figure 9: Survey of habitats with tall grasses using a vehicle.

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The numbers of individuals of each species of mammal counted in a transect were summed and the result divided by the area of the transect to give the density of the species per transect. All densities of species per transect were summed and this was divided by the number of transects surveyed to obtain the mean density per species for the Park. The population of each species was estimated by multiplying its mean density by the area of the Park surveyed. The trend of population was inferred by comparing data from previous studies by Wilson et al. (1993); Bouche (2002, 2006) and Mackie (2004) in the Park.

The biomass density for each species was calculated by multiplying average density of each mammal species by its unit mass (body weight) (Table 3). Unit masses of species were obtained from Kingdon (1997), Kingdon et al. (2013) and Prins and Olff (1998). Total biomass of large herbivores observed in this study was obtained by adding up biomass densities of all species.

Body weight ratio was used to determine the degree of species-packing of the MNP grazers based on the Hutchinson's weight ratio theory (Prins & Olff, 1998; Bonyongo & Harris, 2007). A list of the species of grazers in the Mole National Park and the number of broad habitat types were obtained from the Park's current Management Plan. Biggs (1979) and Bonyongo and Harris provide data for the number of broad habitat types for the Okavango Delta (Botswana); for Kruger National Park, South Africa (Bredenkamp & Brown, 2003); for Etosha National Park, Namibia (Le Roux, Grunow, Morris, Bredenkamp, & Scheepers, 1988); for Kafue National Park, Zambia (Ellenbroek, 1987 and Munyati, 2000); and Hwange National Park, Zimbabwe (Timberlake, 1999). Average body weight

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of each species was obtained by taking the mid-point of weight ranges for both male and female, then averaging them (Prins & Olff, 1998).

Species-packing was evaluated by regressing the natural logarithm of body weight of a species against its rank number in a sequence (showing the largest to the smallest species) from the assemblage of grazers (Prins & Olff, 1998). A plot of natural logarithm of the body weight of a species against its rank-number in the sequence is expected to give a slope of ln 2 (= 0.693) for a sequence in which a species is exactly twice as heavy as the next (Prins & Olff). Under such circumstances the WR equals $e^{\ln 2}$ is 2 and the natural logarithm of body weight of the i^{th} species (Wi) will depend on the rank number (R_i) for a regression line of the function:

$$ln\ (W_i)=aR_i \quad \ldots\ldots (4)$$

where W_i is the body mass of the ith species in the assemblage and R_i its rank number (Prins & Olff, 1998). The WR is then obtained by the function

$$WR=e^a \quad \ldots\ldots (5)$$

Accordingly, the hypothesis of facilitation, competition and coexistence among the grazers (Prins & Olff) and the hypothesis suggesting the importance of habitat diversity in allowing co-existence and grazer community structure (May, 1973) were tested.

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Biotic factors - grass quantity and quality

Grass related factors (grass quantity and quality), are known to be the most important biotic factors accounting for the distribution of wild grazers within a landscape (e.g. Fryxell, 1991; Wilmshurst et al, 2000). In this study, grass quantities were represented by grass biomass (GB) and grass cover (GC), and quality by percentage grass greenness (GG), percentage crude protein (CP) and percentage digestible organic matter (DOM). These were estimated in each habitat of a transect every month. The GC, GG and GB were recorded every 400-500 m from the start of each habitat along each strip transect. A quadrat was thrown randomly from any spot at these intervals along the transect five times to the left and five times to the right. In the case of a point transect a quadrat was thrown four times randomly from central spots within each habitat type. The GC within each throw was calculated using the hundred possible squares obtainable in the quadrat. Also for each throw the GG of grass trapped by the quadrat was estimated. Measurements were averaged to give estimates of GC and GG of a particular habitat. Grass samples were then clipped to ground level from a random throw within feeding sites of each mammal species, dried and weighed for its biomass. Dry samples were then finely ground by a mill and analysed following standard laboratory procedures. The Kjeldahl method (Nielsen, 2010) was used for CP to determine the percentage composition of Nitrogen in the sample. DOM was estimated using the Walkley Black Method to determine the organic carbon content (Walkley & Black, 1934; Allison, 1960; 1965).

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Abiotic and anthropogenic factors

The most important abiotic factors are thought to be water availability and altitude (elevation) (Bailey et al., 1996). Distances of transect habitat and mammal locations from the nearest sources of water were calculated by using the nearest-features extension in ArcGIS (v9.3), after waypoint data stored in GPSs were exported into an ArcGIS (v9.3) environment. Altitude data on transect habitats and mammal locations were transferred from GPSs to a computer. For short habitats along transects, information on the transect habitat location such as GPS reading and altitude were assumed to be the same for their mammal locations. However, because long transects traversed wide distance variations, such information was taken at the location of each mammal.

Human activities may affect species distribution, and so the distributions of mammalsof mammals closer to boundaries, farms or communities was investigated by taking GPS readings of habitats of transects, farms or communities. The distances from a habitat to nearby farms or communities (Community) and also to the nearest boundary of the Park (Boundary) were calculated by using the nearest-features extension in ArcGIS (v9.3) after waypoint data stored in GPSs were exported into an ArcGIS (v9.3) environment.

All data were split into dry, fire, flood and wet seasons for analyses, because different variables may be important in affecting the distribution of mammals in different ways for each of the four seasons.

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Data Management and Analyses

Details of data processing and analyses techniques used are provided below.

General statistics

All data were entered into Microsoft Excel tables (version 2013), before being exported into R statistical software package version 3.1.2 (2014). Microsoft Excel software (version 2013) was used to produce graphs where necessary. In all tests and models throughout this study, $\rho < 0.05$ was used as the criterion for statistical significance, with results being 'highly significant' where $p < 0.01$ or 'very highly significant' where $\rho < 0.001$.

All data were checked for extreme outliers and where none was found and wherever both variables being tested were continuous variables of sufficient sample sizes, Pearson's correlations tests (r) were performed to examine associations between and amongst both response and predictor variables. However, where extreme outliers were found in the data, or sample size was low, Spearman's Rank correlations tests (rs) were performed.

R packages used

The R packages *imputation* (Hastie et al, 1999), *ggplot2* (Wickam, 2009), *GGally* (Schloerke et al., 2014), *reshape* (Wickam, 2007), *reshape2* (Wickam, 2007), *lme4* (Bates, Maechler, Bolker, & Walker, 2014), *nlme* (Pinheiro, Bates, DebRoy, Sarkar, & R Core Team, 2014), *compiler* (R Core Team, 2014), *parallel* (R Core Team, 2014), *multcomp* (Hothorn, Bretz, & Westfall, 2008), *stats* (R

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Core Team, 2014), *pastecs* (Grosjean & Ibanez, 2014), *plotrix* (Lemon, 2006), *calibrate* (Graffelman, 2013), *xts* (Ryan & Ulrich, 2014), *tseries* (Trapletti & Hornik, 2015), *forecast* (Hyndman, 2015; Hyndman & Khandakar, 2008), and *boot* (Canty & Ripley, 2014) were used.

Time series analyses

Rainfall, temperature and land cover change data over a period spanning 1980-2013 were analysed using time series statistics with R to establish the relationships among them, to model them with ARIMA model, and if possible, forecast next observations in the time series.

There are many different packages for time series analyses but the *xts* package was used for the time series data representation (object class) because it is versatile enough for time series data structure. The *xts* package is actually a superset of the *zoo* package and, therefore provide the same results. However, *tseries* and *forecast* packages were also used for their appropriate analyses as was necessary. Autocorrelations and partial autocorrelations were calculated using the autocorrelation function (*ACF*) and partial autocorrelation function (*PACF*) respectively from the *xts* package. The presence of autocorrelations is one step forward in the time series analysis as it indicates that an autoregressive integrated moving average (ARIMA) model could model the time series.

The ARIMA model includes the model order, p, d, q, and the first (and most important) step in fitting an ARIMA model is the determination of the order of differencing, d, needed to make the series stationary (i.e. the probability

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distribution does not change with time). At the lowest order of differencing the time series is expected to fluctuate around a certain mean value and its *ACF* plot approaches zero rapidly. The number of significant autocorrelations in the *ACF* output was estimated as the number of moving average (MA) coefficients, q, and from the *PACF* output the number of autoregression (AR) coefficients, p was estimated. The cross-correlation function (*CCF*) was used to deduce the presence of lagged correlations between mean rainfall time series and mean temperature time series; mean rainfall time series and land cover changes time series, between time series of land cover variables etc. over the time frame. Also, the Ljung–Box test function from the *xts* package, which implements the Box–Pierce statistical test was used to test the time series for the presence or absence of autocorrelation (or partial autocorrelation) when samples are small (Box & Pierce, 1970; Ljung & Box, 1978; Harvey, 1993). The test is recommended because it assesses departures from random expectation across the whole set of specified lags (i.e. correlation between the measure at time t with that at t-1, t-2, t-3, etc.) rather than testing 'significance' at each lag separately.

Forecast by ARIMA modelling (the Box–Jenkins approach) has three stages: model identification (fitness), parameter estimation, and diagnostic checking, which run repeatedly to obtain a model that suits the given data for time series prediction. The ARIMA model was fitted to the rainfall and temperature time series data using the *arima* function in the *forecast* package to estimate the coefficients, standard errors and confidence intervals. After validating the ARIMA model, the *predict* function was used in the *forecast* package to forecast

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the observations for the annual mean rainfall and annual mean temperature time series in the next seven years (up to 2020). As it was necessary to test whether the mean rainfall or the mean temperature time series was mean reversible or random walk, the Augmented Dickey–Fuller (ADF) test (Said & Dickey, 1984) was used, which is implemented by the *adf.test* function of the *tseries* package. From the output of the Dickey–Fuller test one can ascertain the presence or otherwise of a unit root in an autoregressive (AR) model. A simple AR (1) model is

$$y_t = by_{t-1} + u_t, \quad \text{..... (6)}$$

where y_t is the variable of interest, y_{t-1} is the time index, b is a coefficient, and u_t is the error term. A unit root is present if the $b = 1$ and the model would be non-stationary. The output from *adf.test* includes a *p*-value. Conventionally, if $p < 0.05$ then the time series is supposed to be mean reverting whereas a $p > 0.05$ may indicate the time series is a random walk (Dickey & Fuller, 1979; Said & Dickey, 1984; Enders, 2010).

Spatial analysis

All waypoints stored in the GPSs were downloaded and processed using Map Source (Garmin Limited, version 6.13.7) and GPS Utility (GPS Utility Limited, version 4.99). The Geographical Information Systems software ArcGIS (v9.3) was used for spatial analysis, particularly in generating a number of response variables, and to produce all the maps.

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Generalised linear model (GLM)

The aim of the implementation of the GLM was to model mammal count, density or presence/absence (response variable) as a function of ecological parameters recorded (explanatory variables) including (i) habitat type, (ii) season, (iii) grass quantity, (iv) grass quality, (v) elevation, (vi) anthropogenic factors, and (vii) nearest distances from water sources. The idea behind this analysis was to investigate how these factors affected the distribution and abundance of the mammals using count or presence/absence data as a function of distribution for each of eight large sympatric grazers, namely, elephant, buffalo, roan antelope, waterbuck, hartebeest, kob, warthog and bushbuck. Habitat quantity was represented independently by grass biomass (GB) and percentage grass cover (GC), and grass quality likewise by percentage grass greenness (GG), percentage digestible organic matter (DOM) and percentage crude protein (CP).

Two of the variables, DOM and CP made the data imbalanced as there were only 464 events for each unlike the 1391 for the other variables. This would restrict the data in all analyses involving any of them to only 464 events that is unfair to the effort made as well as biasing the results. To address this problem, 'k nearest neighbour imputation' in the *kNNimpute* function of the *DMwR* package was used to replace the missing values in only the two variables DOM and CP and created a new data frame.

Data exploration

Graph visualization showed too many zeros in the count data that it was hard to see what the distribution of the other values were until both axes were log-

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transformed (Figures 10-12) using log (1+x) instead of log x because x is zero in many cases. There was also a problem with the data being very spread out. Some transects had considerably higher values than others indicating that serious problems with homogeneity can be expected if mixed effects modelling is applied. Ignoring this problem may result in regression parameters with incorrect standard errors, an F statistic no longer F distributed and the t statistic not following a t distribution. This invalidates the statistics used in assessing statistical significance. One option for addressing this problem is to use different variances per transect, but the variance would expand inconveniently. Again, there was imbalance in variable data from the different transects, that might lead to estimation of multiple variances with generalised least squares (GLS) being unstable. A square root transformation was attempted, but the variances were still not homogeneous enough so modelling counts with a Poisson error was preferred. As mixed modelling is the optimal statistical technique to analyse these data, because they are unbalanced but with a sufficiently large sample size to ensure convergence of maximum likelihood estimates, a generalised linear mixed effect model (GLMM) with a Poisson distribution is appropriate. The raw mammal counts were used in preference to mammal density because the density was calculated from the count data and so introduces an additional source of error (the area estimate).

Mixed effect models

The number of zeros was far higher than a Poisson, or even a negative binomial distribution. This looked very much like a mixture of two distributions

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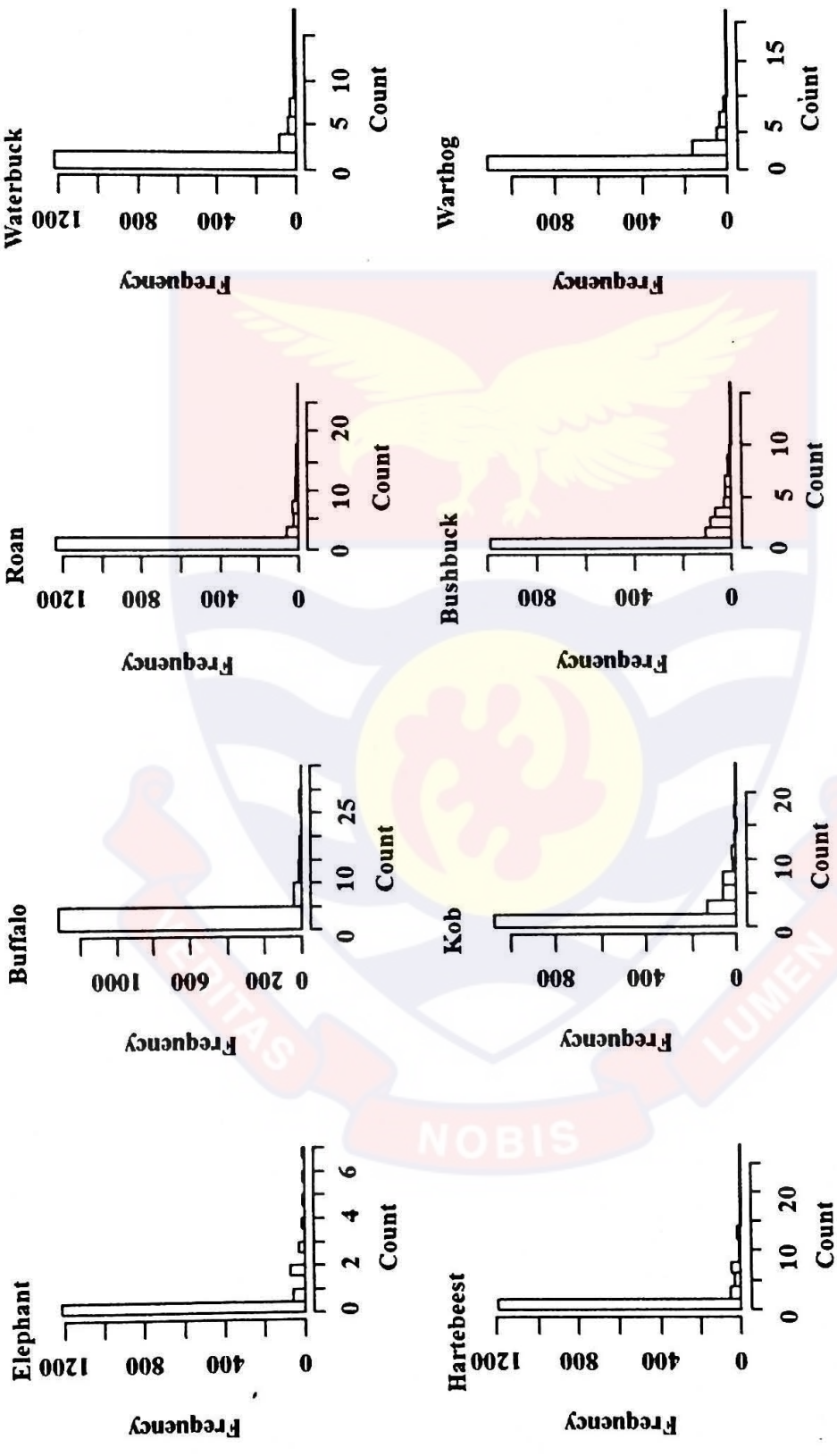


Figure 10: Distribution data for each grazer species (N = 1392).

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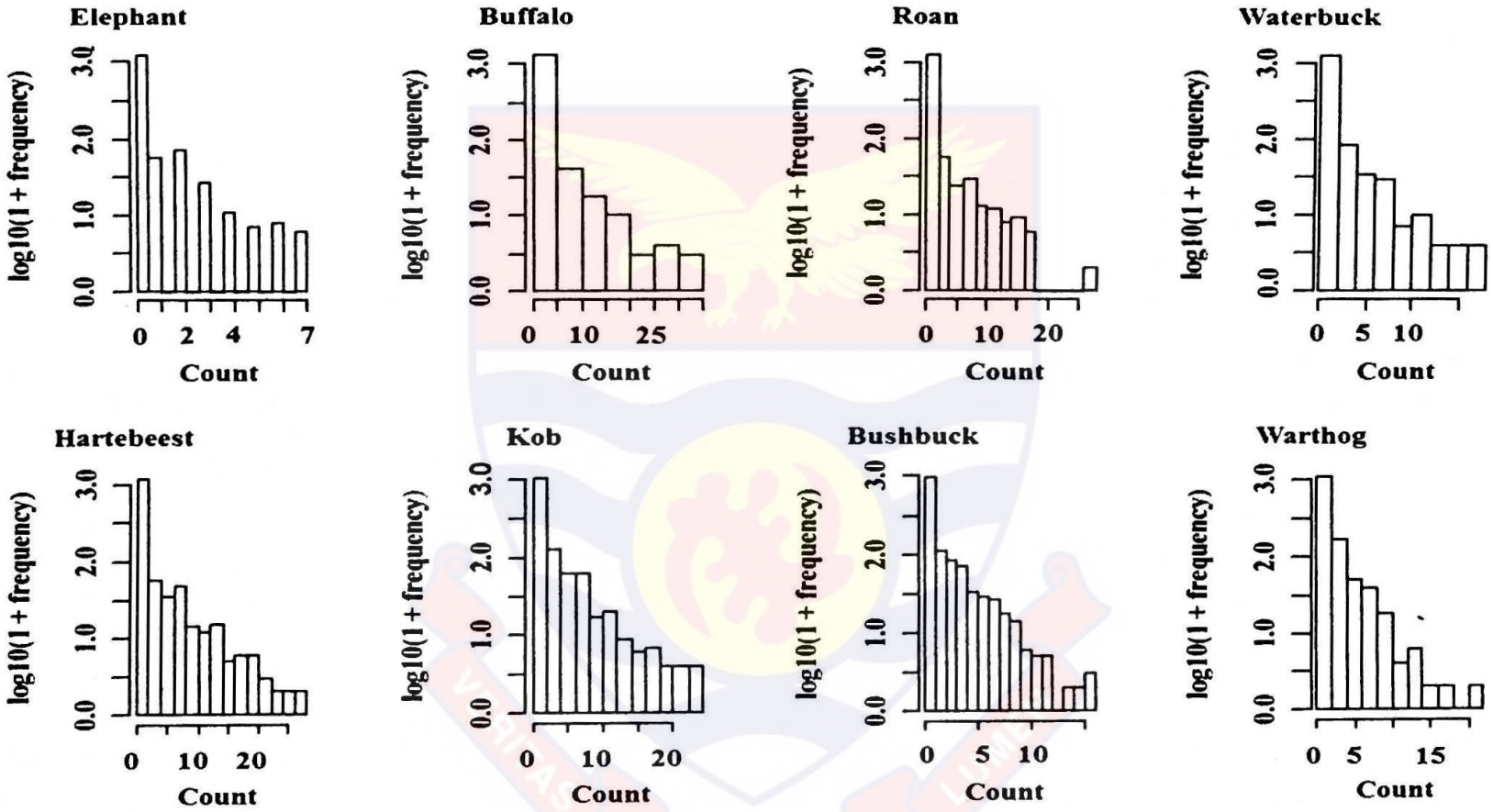


Figure 11: Distribution data for each grazer species after log-transforming the y-axis (N = 1392).

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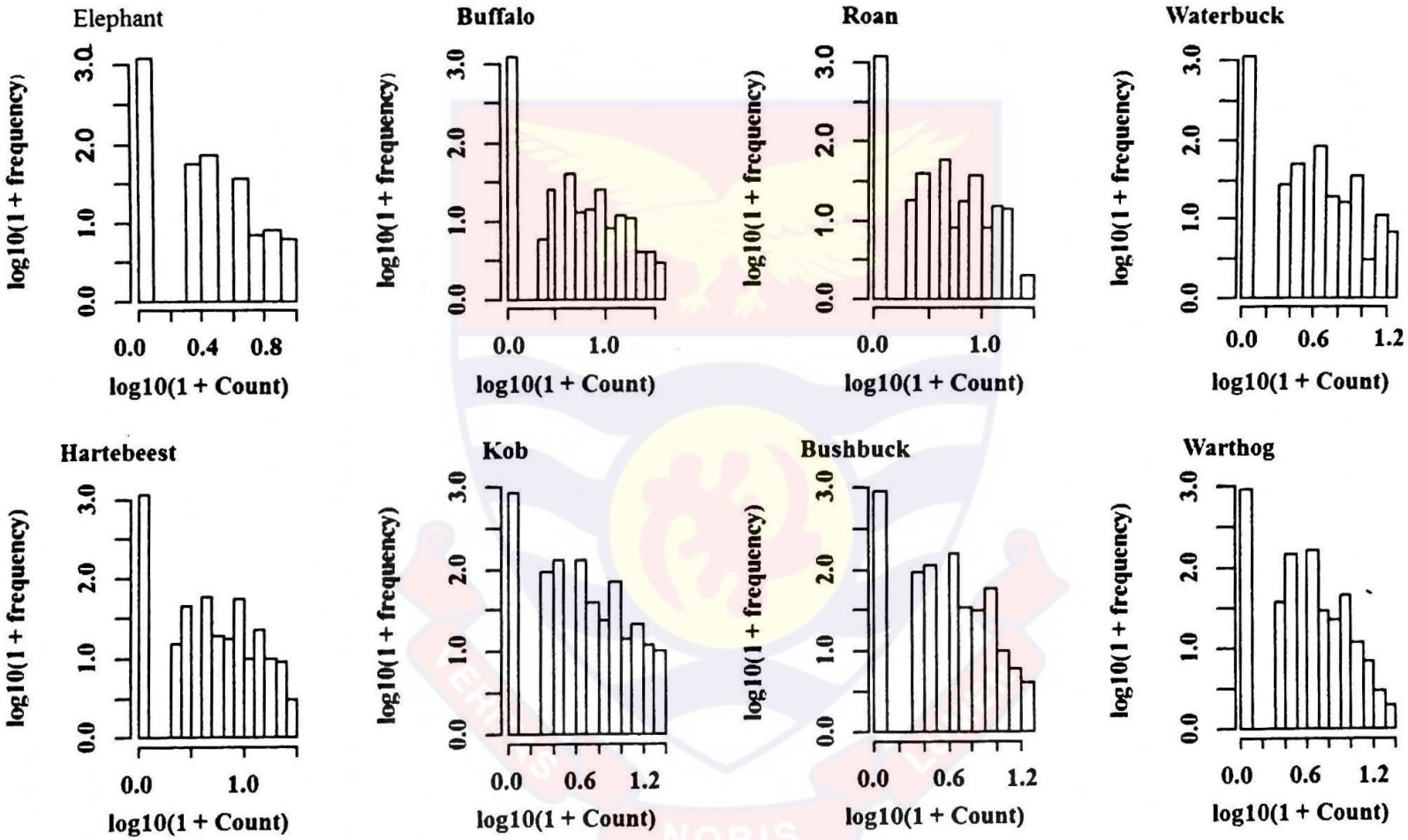


Figure 12: Distribution data for each grazer species after log transforming both axes (N = 1392).

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where in some transects, the animals never occurred while in others they occurred with a certain probability. This is a zero-inflated distribution, with greater over-dispersion than would be expected from Poisson. Since there is no zero-inflated mixed model, the best solution is to analyse count and presence/absence data separately. Therefore, a generalised linear mixed effect model (GLMM) with a Poisson distribution was used to analyse the count data and mixed effects logistic regression model to analyse presence/absence data. Mixed effects logistic regression is used to model binary outcome variables, in which the log odds of the outcomes are modeled as a linear combination of the predictor variables when data are clustered or there are both fixed and random effects.

The mixed effects model is applied using the *lme* function, which stands for linear mixed effects model, in the *lme4* package. In the *lme* function, the random component has to be specified (Zuur, Ieno, Walker, Saveliev, & Smith, 2009). The "1 | Transect" component specifies a random intercepts model. The argument on the right hand side of the '|' sign is a nominal variable, or transect in this case.

The explanatory variable of a GLMM combines the fixed effect and the random effects components, and it is generally represented by the equation:

$$Y_i = X_i \times \beta + Z_i \times b_i + \varepsilon_i \quad \ldots\ldots(7)$$

$b_i \sim N(0, D)$, $\varepsilon_i \sim N(0, \Sigma_i)$ and $b_1, \cdots b_N$, $\varepsilon_1, \cdots, \varepsilon_N$ independent.

Y_i is the response variable that contains mammal count or presence/absence values for transects i, $i = 1, 2$ ..... and 36. The $X_i \times \beta$ represents the fixed part of

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the model and $\mathbf{Z}_i \times \mathbf{b}_i$, the random part. N (0, D) is the assumption that the random effects $\mathbf{b}i$ are normally distributed and the errors εi (the noise), which are the within-transect variations are also assumed to be independently normally distributed with covariance matrix Σi, with mean, 0 and variance, σ^2. The selection approach for linear mixed effects models should broadly follow a protocol consisting of 10 steps (Zuur et al., 2009). This involves starting with a model with as many explanatory variables as possible (in the fixed part of the model) as step 1, then finding the optimal random structure (steps 2–6), the optimal fixed structure (steps 7–8), presenting the results of the optimal model (step 9), and finally, giving an interpretation (step 10). I followed these steps in another way, by listing all possible model formulae taking fixed and random effects into account and by using the function *glmer* from the R package lme4 to fit the models. In *glmer* you do not need to specify whether the groups are nested or cross-classified, R can determine it based on the data. The same (1 | Transect) general syntax was used to indicate the intercept (1) varying by "Transect".

Just like step 1 of the protocol (Zuur et al., 2009), the initial model consisted of two categorical predictors "season" and "habitat types" with four and six levels respectively, and nine continuous predictor variables, "GG", "GB", "GC", "DOM", "CP", "Elevation", "bdry", "water", and "cty" all in the fixed model; and "transect" and "study site" in the random model. Model formulae were different by one or the other categorical predictor in the fixed or random models and also by one or more continuous variables. The necessity to visualize the continuous variables in order to understand the distributions and relationship

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among the variables, and excluding co-linearity to make sure the predictors appear independent of each other, informed the use of *GGpairs* function (from the *GGally* package; Schloerke et al., 2014) to plot a graph of the continuous predictor variables. Booth, Niccolucci, and Schuster (1994) suggest that correlations between pairs of variables with magnitudes greater than ± 0.5 indicate high collinearity, and the same rule-of-thumb was used.

As the large grazers' resource locating distances are expected to be substantially smaller than the spatial extent of the study area, spatial auto-correlation between transects is possible. Spatial auto-correlation in the presence/absence data could be seen if the pattern of habitat distribution is spatially auto-correlated. However, autocorrelation is of less concern for the following reasons (i) large number of explanatory variables were expected to account for most of the spatial auto-correlation once the model is fitted to the data and ii) since the data were nested and the spatial scale of nesting coincides with the spatial scale of auto-correlation using GLMM (McCulloch, Searle & Neuhaus, 2001) will deal with spatial auto-correlation within transect. These approaches would also take account of dependencies within and between sites.

The different models were then compared by the *anova* command. A model's fitness was assessed by the AIC and p-values. Unfit models and predictors that were not statistically significant were removed to obtain the optimal model to equal steps 2-9 of the protocol described in Zuur et al. (2009). Boxplots were used to look at the distribution of the continuous variables at each level of the binary outcome for each response variable.

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CHAPTER FOUR: RESULTS

Climate and Land Cover

From descriptive statistics, the decade mean of temperature for the 2000s (2000–2010) was the highest (27.2 ^{0}C ± 0.15 ^{0}C; range = 24.7-31.5 ^{0}C) followed by the 1990s (1990–1999) with 27.1^{0}C ± 0.15 ^{0}C (range = 24.4-31 ^{0}C) and the least of 26.7 ^{0}C ± 0.25 ^{0}C (range = 24.3-32.7 ^{0}C) in the 1980s (1980-1989). Results of ANOVA revealed the differences in the three decade mean temperatures were significant, $F(2, 360) = 3.49$, $\rho < 0.05$, but Tukey's post-hoc analysis indicated the differences were only significant between the 1980s and 2000s (Tukey's pairwise = 3.58, $\rho < 0.05$). The decade mean of rainfall for the 1980s was the highest (129 mm ± 9.91 mm, range = 0-362 mm) followed by the 1990s with 95.9 mm ± 10.17 mm (range = 0–390.4 mm) and the least of 93.9 mm ± 7.41 mm (range = 0-304.1 mm) in the 2000s. ANOVA results indicated the differences in the three decade mean rainfall values were significant, $F(2, 357) = 4.54$, $\rho < 0.05$; Tukey's post-hoc analysis indicated the differences is significant between the 1980s and 1990s (Tukey's pairwise = 3.58, $\rho < 0.05$) and between 1980s and 2000s (Tukey's pairwise = 0.99, $\rho < 0.05$) only.

Figure 13 shows a negative correlation between the mean rainfall time series and the mean temperature time series ($r = -0.511$) for the period under review from 1980 – 2013. The estimated value from the series' cross-correlation

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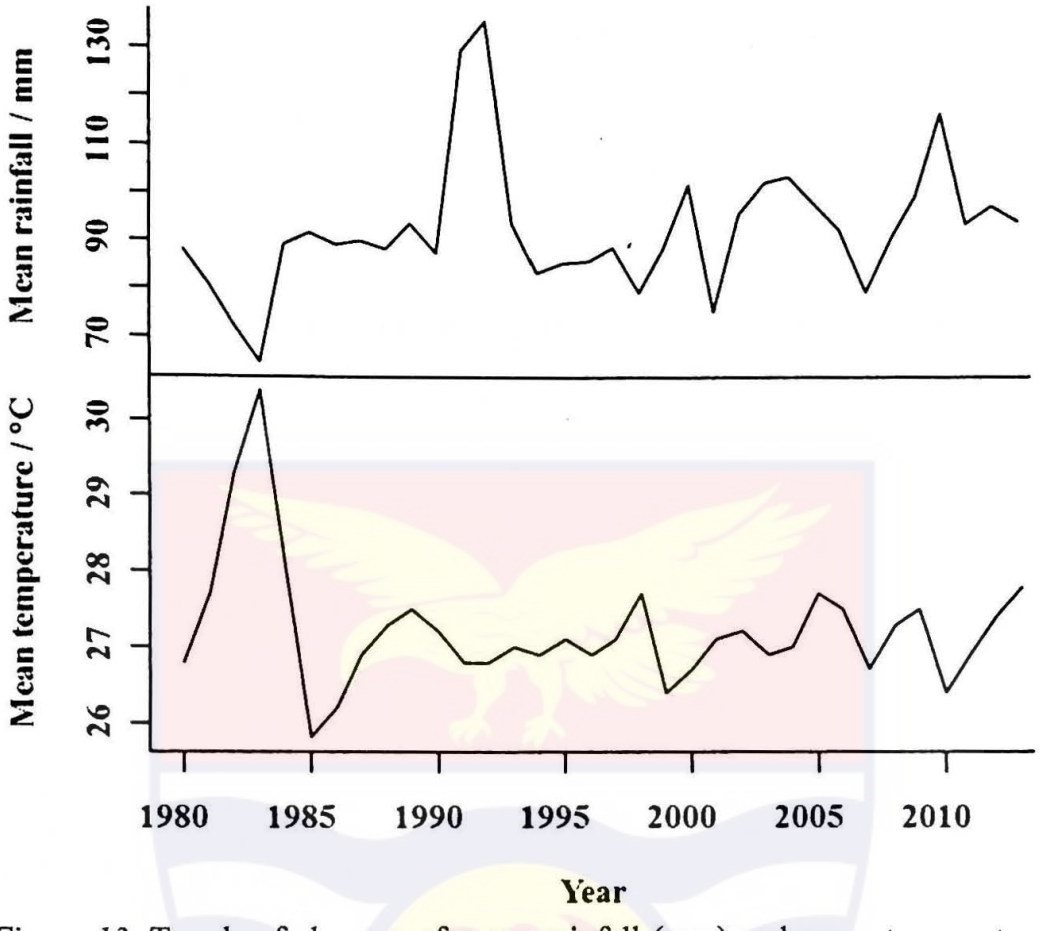


Figure 13: Trends of changes of mean rainfall (mm) and mean temperature (^{0}C) from 1980 – 2013 at MNP.

function (CCF) revealed the relationship between the trends of changes of mean rainfall and mean temperture was significant (Figure 14). When the mean rainfall decreased, the mean temperature rose. Furthermore, Box-Ljung test indicated highly significant autocorrelations for the mean rainfall time series ($\chi^2 = 6.95$, df = 1, ρ-value = 0.008) and the mean temperature time series ($\chi^2 = 9.14$, df = 1, ρ-value = 0.002) to confirm their suitabilities for time series analysis.

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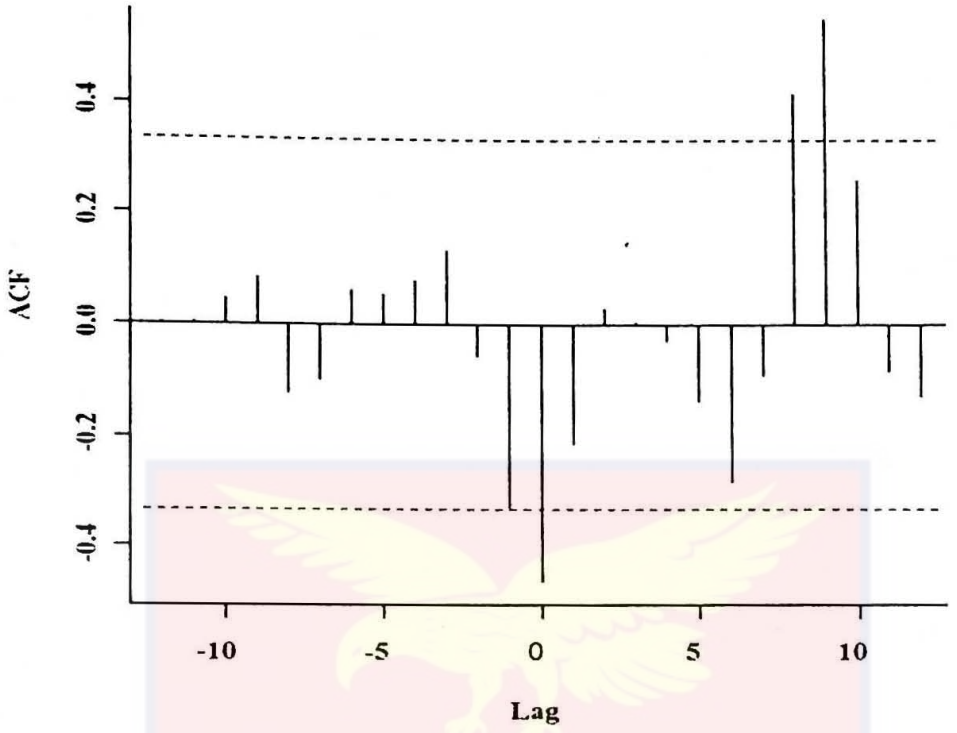


Figure 14: Cross correlation function between mean rainfall and mean temperature time series from 1980 – 2013 showing correlations are significant at lags 8 and 9 which cross the dash line.

From the ACF for mean rainfall time series (Figure 15), the moving average (MA) was one and this suggested that its ARIMA model would require one MA coefficient {MA(1)} (i.e. q in the model order = 1). The time series partial ACF (Figure 16) showed there was one lag value that was statistically significant so the initial model would have one AR coefficient {AR(1)} (i.e. p in the model order = 1). The *difference* function revealed zero difference and this suggested that d in the model order is 0. The model assumed that the original series was stationary (mean-reverting, Dickey-Fuller = -3.0473, Lag order = 3, ρ = 0.017). It appeared this was a slow-speed mean reversion. As the ACF and the partial ACF results (Figures 15 and 16, respectively) were a little difficult to interpret, *auto.arima* function confirmed the best order for (p, d, q) in the ARIMA

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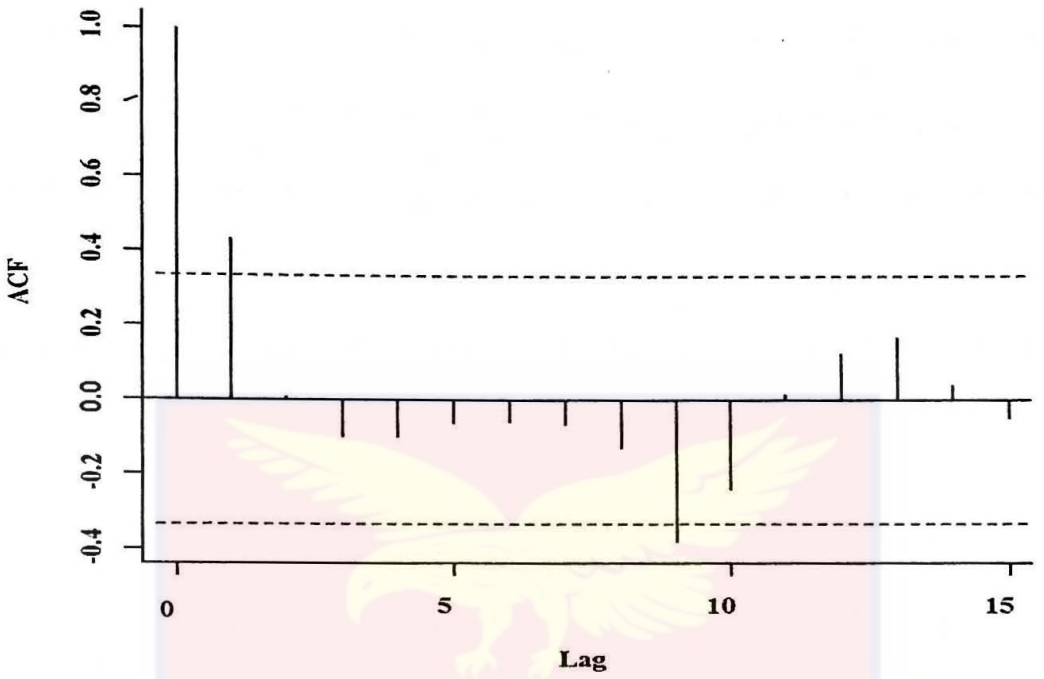


Figure 15: Autocorrelation of mean rainfall time series from 1980–2013 showing it is significant at lag 9 which crosses the dash line as lag 1 is too close to zero.

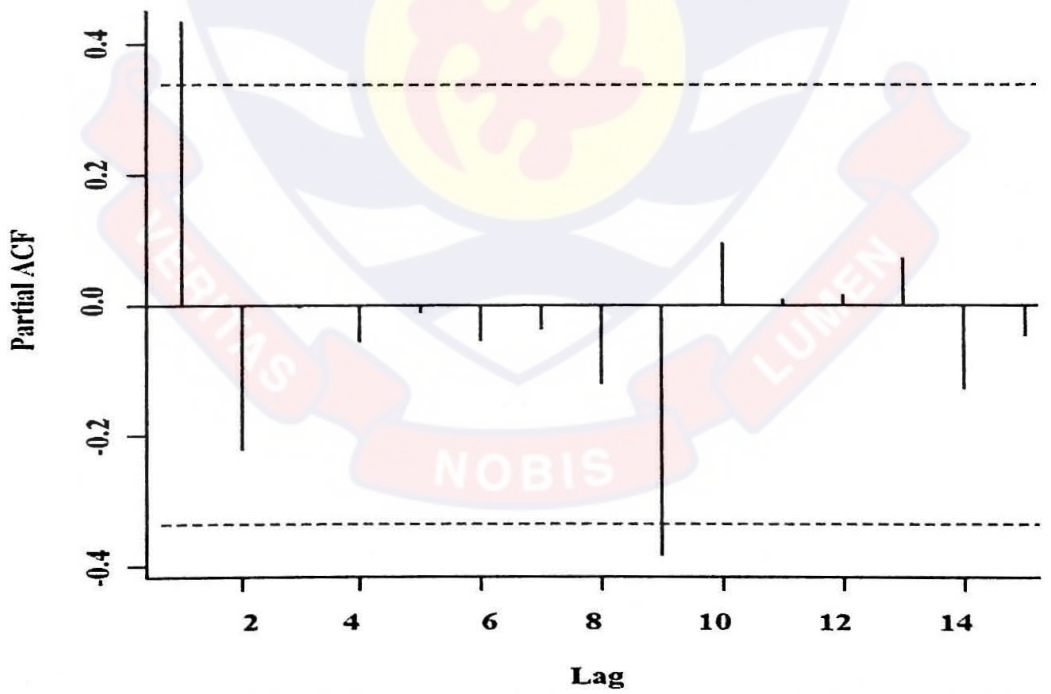


Figure 16: Partial autocorrelation of mean rainfall timeseries from 1980–2013 showing it is significant at lag 9 which crosses the dash line as lag 1 is too close to zero.

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model as (1, 0, 1). The mean rainfall data series fitted the model because the *tsdiag* function for model diagnostics, fitness and validation indicated standardized residuals did not show clusters of volatility (Figure 17), the autocorrelation function (ACF) showed no significant autocorrelation between the residuals (Figure 17), and the *p*-values for the Ljung–Box statistics were all large (Figure 17), indicating that the residuals were patternless: only "noise" remained.

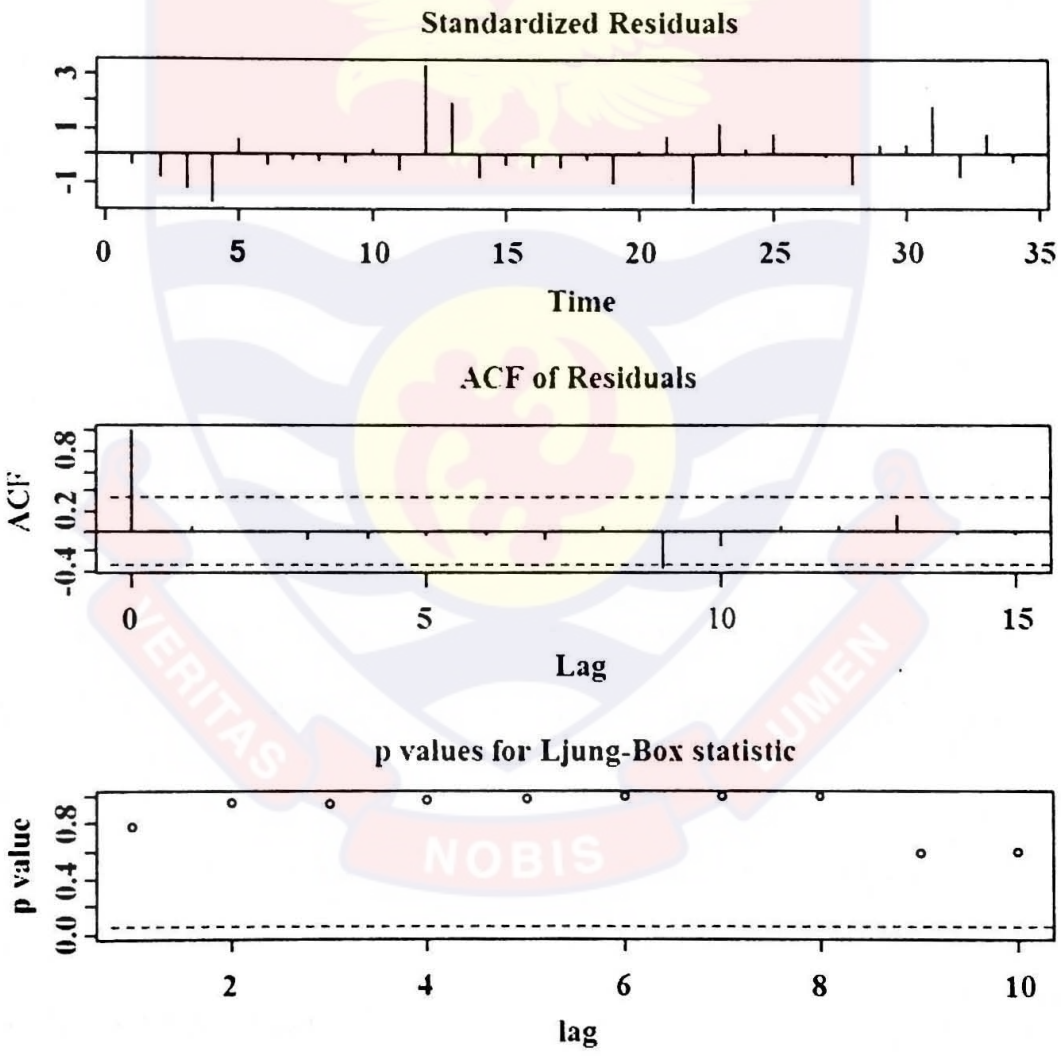


Figure 17: Graphical results of model diagnostics by Ljung–Box statistics of the ARIMA model for mean rainfall time series showing the model is a good fit.

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From the ACF for mean temperature time series (Figure 18), estimated *q* in the model order = 0. The time series partial ACF (Figure 19) indicated *p* in the model order = 2. The *difference* function revealed *d* in the model order = 0. The model assumed that the original series was stationary (mean-reverting, Dickey-Fuller = -5.581, Lag order = 3, ρ -value = 0.01). *Auto.arima* function confirmed the best order was (2, 0, 0) in the ARIMA model, and the mean temperature data series fitted the model because the *tsdiag* function for model diagnostics, fitness and validation indicated that standardized residuals did not show clusters of volatility (Figure 20), the autocorrelation function (ACF) showed no significant autocorrelation between the residuals (Figure 20), and the *p*-values for the Ljung–Box statistics were all large (Figure 20), indicating that the residuals were patternless.

Forecasting

Figure 21 shows the results of a forty-year trend of changes between rainfall and temperature (from 1980 to 2020) including a seven-year forecast period from 2013 to 2020. While the mean annual rainfall is expected to remain low over the period between 2013 and 2020, the mean annual temperature is expected to remain high. The trend also indicated the possibility that, in future, the mean annual rainfall will rise and the mean annual temperature reduce as expected of time series that were mean reverting and so had the potential to return to their averages in future.

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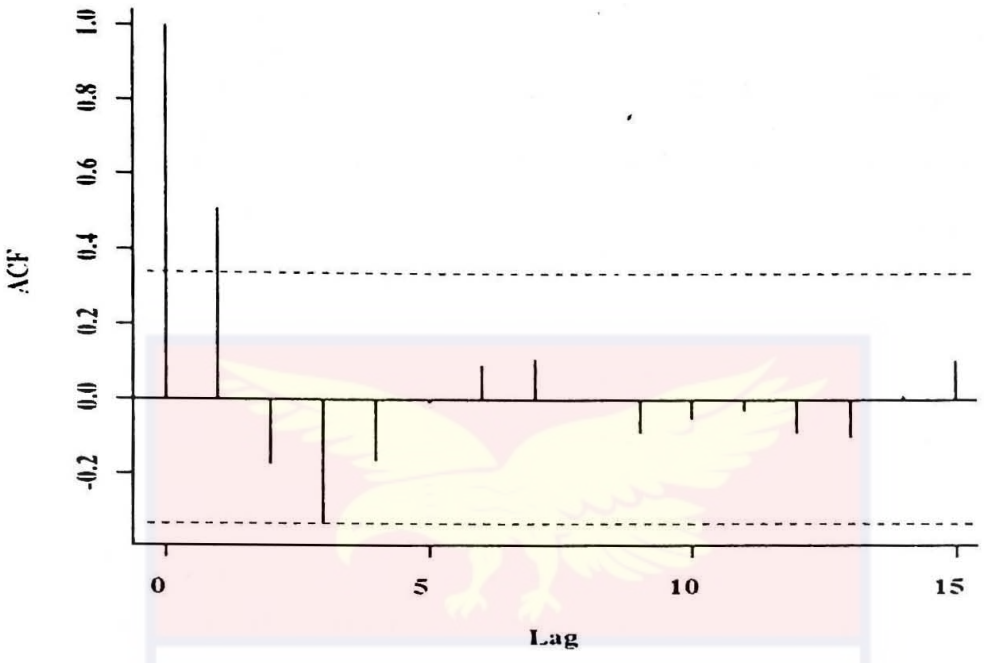


Figure 18: Autocorrelation of mean temperature time series from 1980–2013 showing it is significant at lag 3 which cuts the dash line as lag 1 is close to zero.

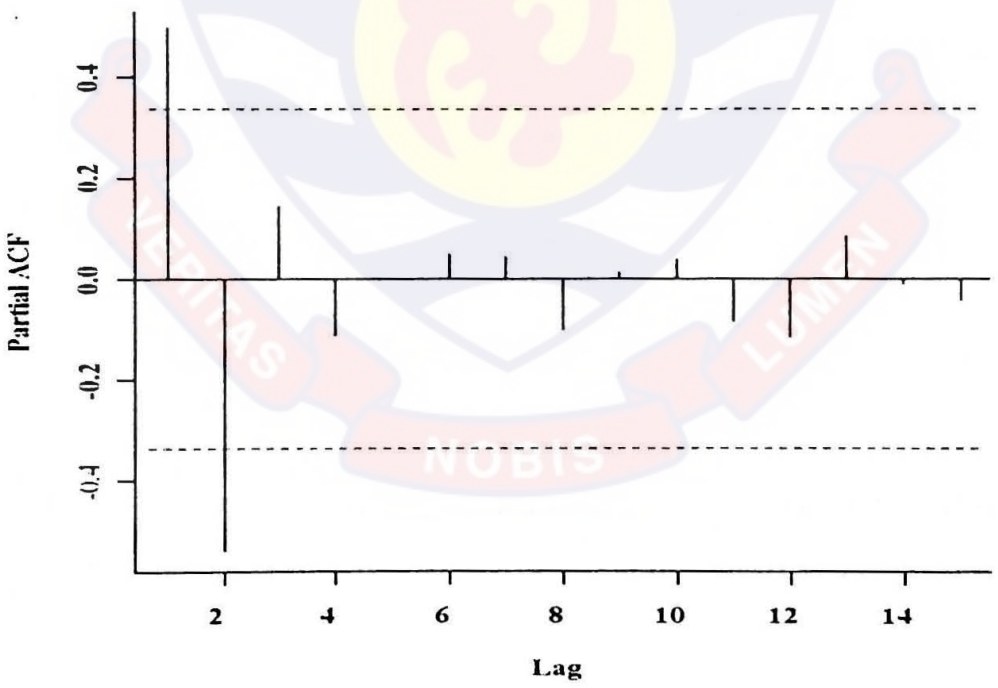


Figure 19: Partial autocorrelation of mean temperature time series from 1980–2013 showing it is significant at lag 2 which crosses the dash line as lag 1 is close to zero.

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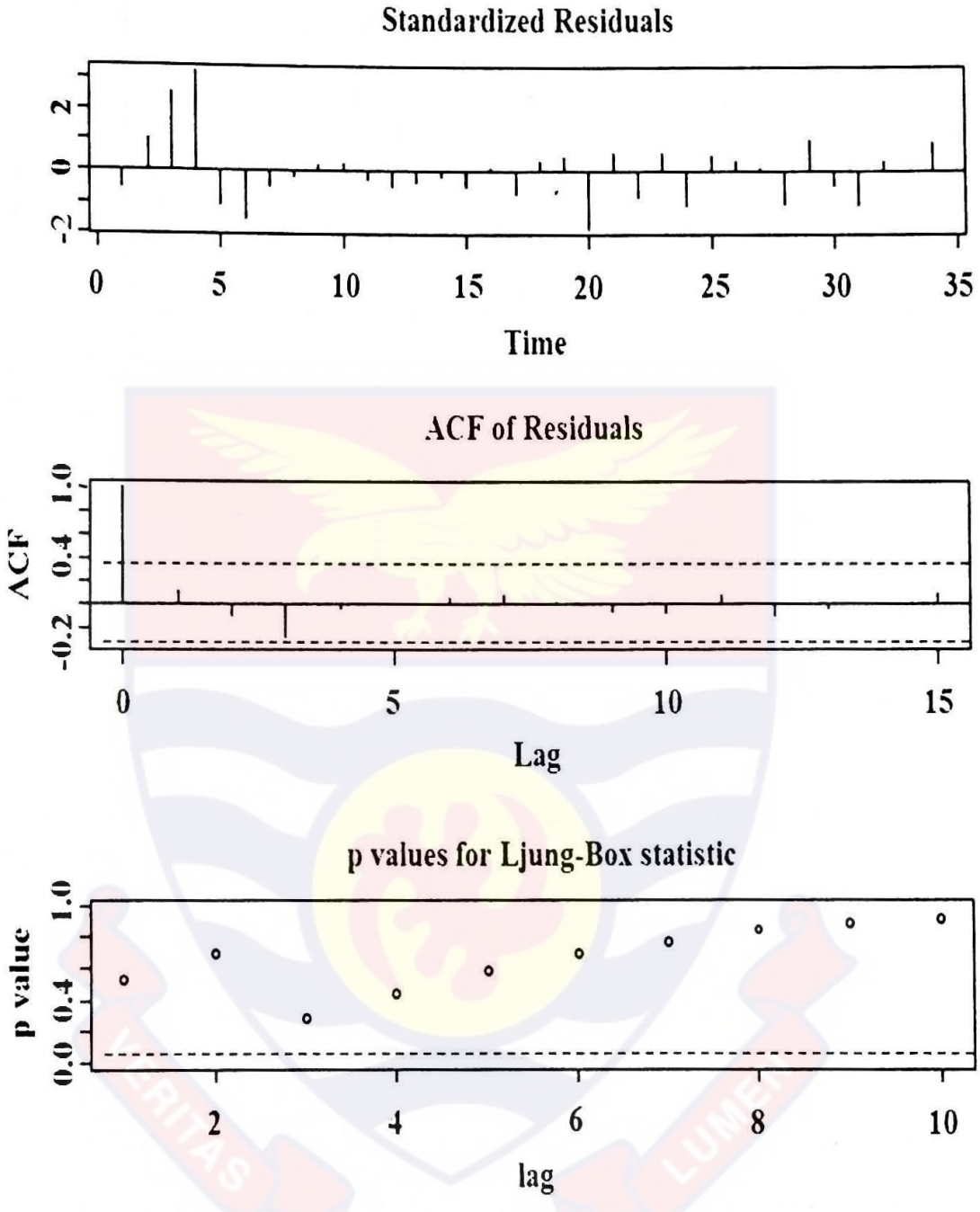


Figure 20: Graphical results of model diagnostics by Ljung–Box statistics of the ARIMA model for mean temperature time series showing the model is a good fit.

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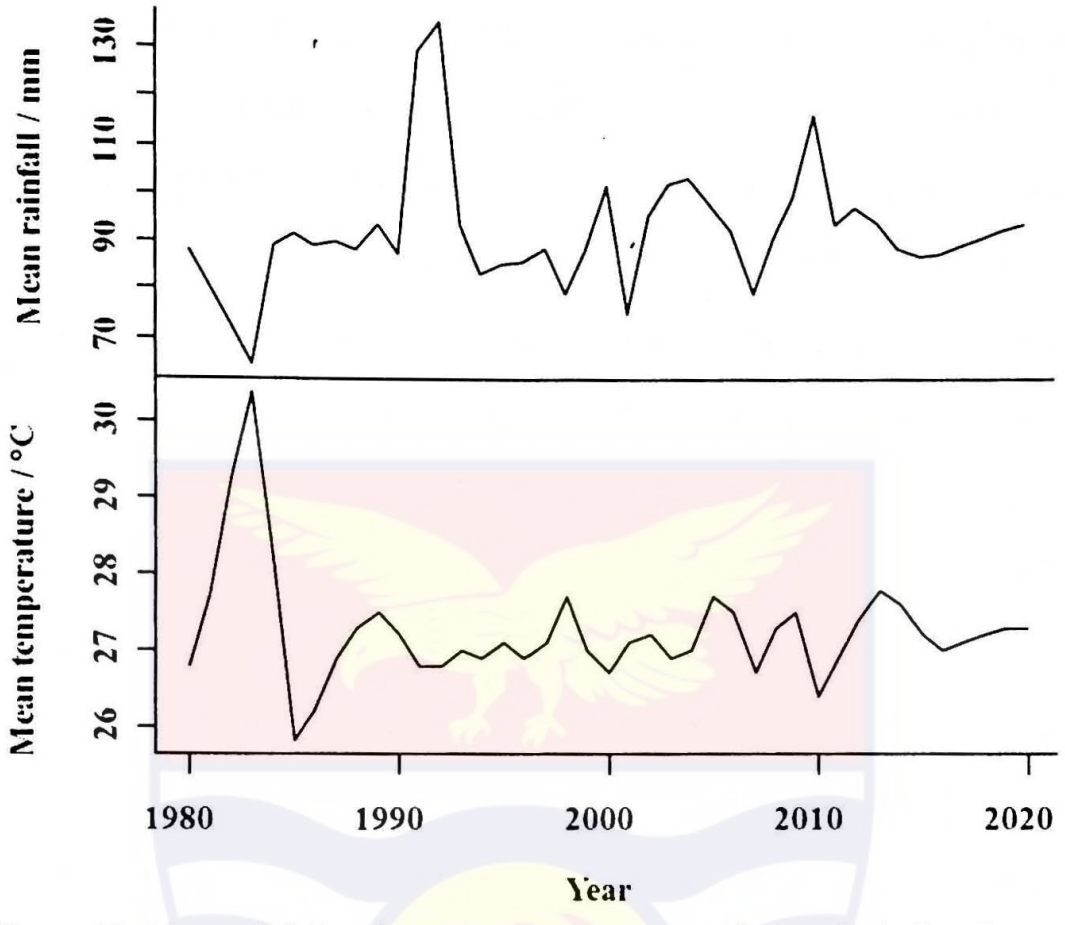


Figure 21: Mean rainfall and mean temperature over 40 years including forecast period up to 2020.

Imagery, matrices of land cover and ground truth accuracy assessment

Figures 22-23 show Landsat satellite imagery for the years 1980 and 1985, 1990 and 1995, 2000 and 2005, and 2010 and 2013 respectively; Table 6 shows the matrices of land cover by class values for the years 1980, 1985, 1990, 1995, 2000, 2005, 2010 and 2013 obtained from Landsat satellite imagery; and Table 7 displays results of ground truth accuracy assessment of the 2010 imagery. An overall accuracy of 80.3% and class accuracy ranging from 71.67–88.33% were high enough to validate the imagery. Therefore the matrix of land cover by class values shown (Table 6) were reasonable estimates of land occupancy by the

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various land cover classes in the MNP. Analysis of variance (ANOVA) indicated very highly significant difference among the various land cover classes ($F(4, 35) = 29.358$, $\rho < 0.001$), and Tukey's *post hoc* analysis indicated that there was a very highly significant difference between six out of the 10 pairs of the five different land cover classes: these were between grass/herbaceous and bare/built-up area (465.6, C.I = 264.4-667, $\rho < 0.001$); between open savanna and bare/built-up area (482.6, C.I. = 281.4-683.8, $\rho < 0.001$); between shrubs/herbaceous and bare/built-up area (632.6, C.I. = 431.4-833.8, $\rho < 0.001$); between grass/herbaceous and closed savanna (349.625, C.I. = 148.4-550.8, $\rho < 0.001$), between open savanna and closed savanna (366.6, C.I. = 165.4-567.8, $\rho < 0.001$), and between shrub/dense herbaceous and closed savanna (516.6 C.I. = 315.4-717.8, $\rho < 0.001$). There was no significant difference between closed savanna and bare/built-in area, open savanna and grass/herbaceous; shrubs/herbaceous and grass/herbaceous; and between shrubs/herbaceous and open savanna.

The shrub/herbaceous class occupied the largest part of the Park (1,261 km^2), constituting 26% of the Park's total area (Table 6), followed by the open savanna, with an average of 1,111 km^2 (23% of the Park's area) and the built-up with an average of 629 km^2 occupied the least area of 13% (Table 6).

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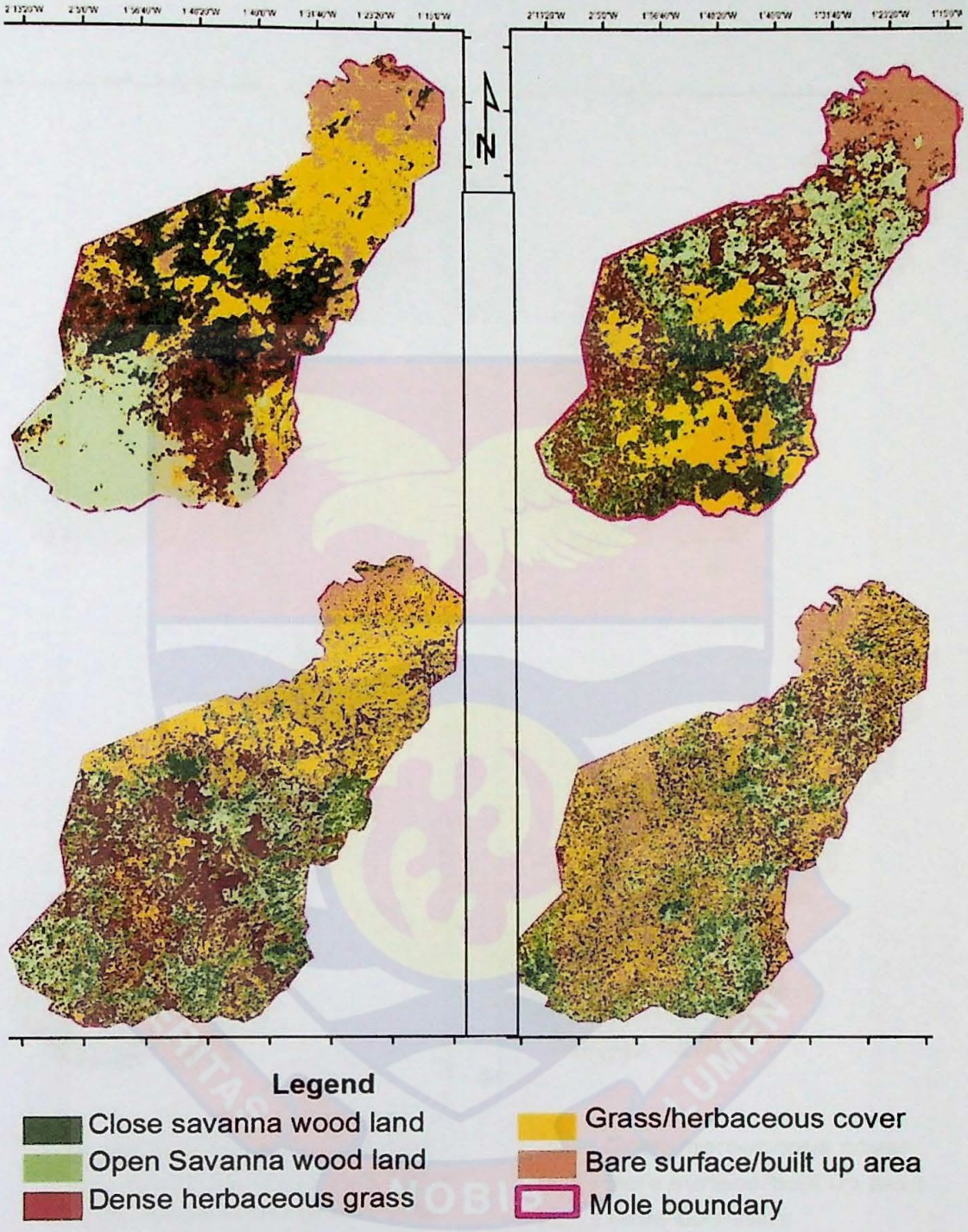


Figure 22: Landsat satellite images for the years 1980 (top left), 1985 (top right), 1990(bottom left) and 1995 (bottom right).

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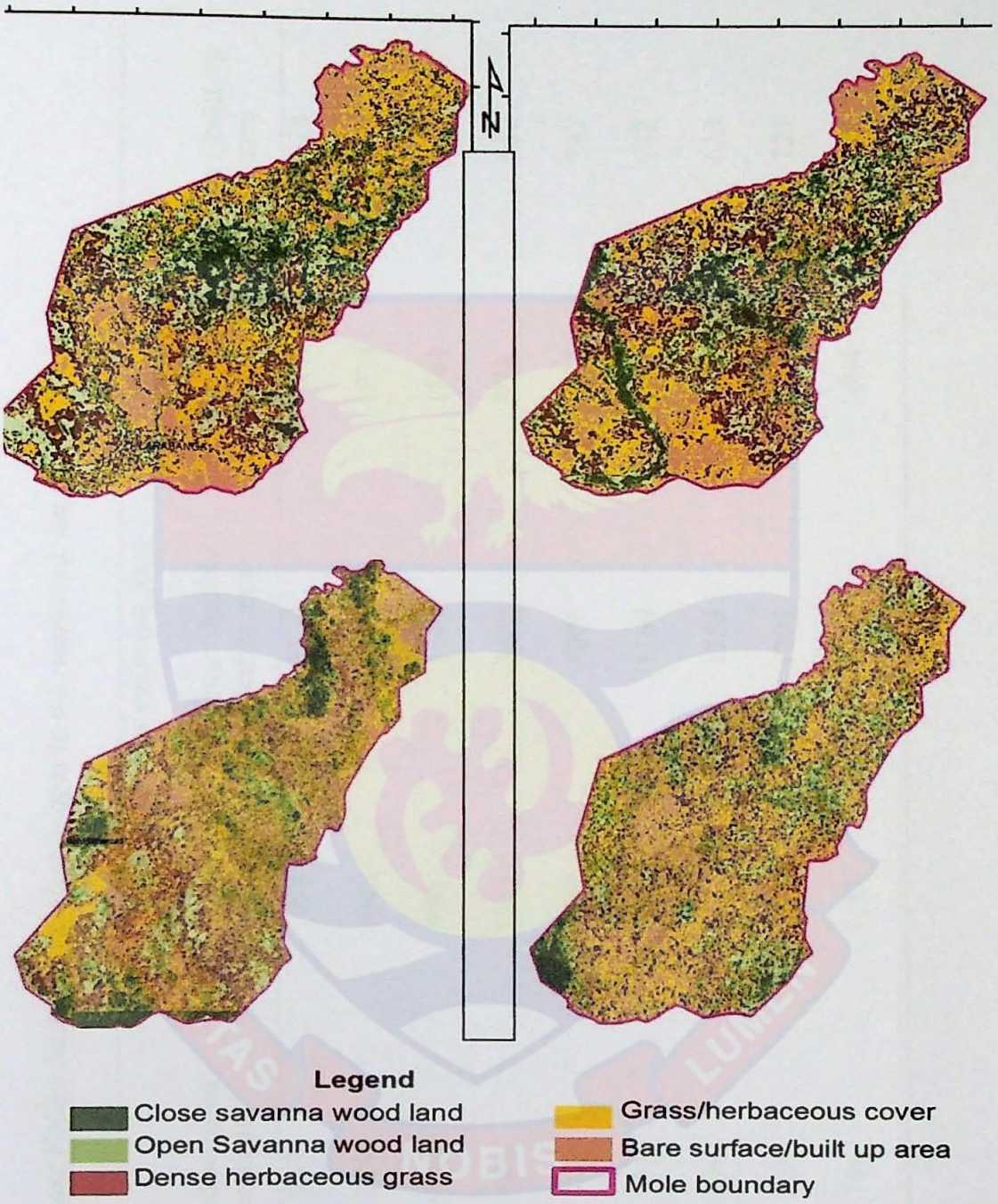


Figure 23: Landsat satellite images for the years 2000 (top left), 2005 (top right), 2010(bottom left) and 2013 (bottom right).

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Table 6

Matrix of Land Cover by Class Values based on Landsat Images to the nearest sq. km

Year	Class value (sq. km)				
	Closed savanna woodland	Open savanna woodland	Dense shrubs / herbaceous	Grass / herbaceous	Bare / built-up area
1980	959	1098	1124	1031	628
1985	889	1046	1191	1074	640
1990	688	996	1587	1301	267
1995	592	1211	1454	926	657
2000	791	1192	1006	1103	747
2005	773	1123	1169	1032	742
2010	698	1020	1353	1145	623
2013	566	1203	1205	1141	724
Average	744	1111	1261	1094	629

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Table 7

Ground Truth Data Assessing the 2010 Landsat Satellite Image in 2012/2013

Class	Closed savanna woodland	Open savanna woodland	Shrub/dense herbaceous	Grass / herbaceous	Bare / built-up areas
Closed savanna woodland	52	8	0	0	0
Open savanna woodland	6	44	5	5	0
Shrub/herbaceous	1	3	49	7	0
Grass/herbaceous	1	5	4	43	7
Bare/ built-up areas	0	0	2	5	53
Sum	60	60	60	60	60
Class accuracy (%)	86.67	73.33	81.67	71.67	88.33
Overall accuracy (%)	80.33				

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Land cover time series

Both ACF and PACF of each of the land cover class values time series and the CCFs of all 10 pairs of the five classes were not significant, meaning that ARIMA models could not be used to model the land cover class values as a time series. Again, neither rainfall time series nor temperature time series cross-correlated with any of the land cover class values time series. The land cover data had only eight events, and therefore may be too small for effective statistical analysis. However, there appeared to be a somewhat consistent trend of land cover changes with rainfall over the years (Figure 24). For example, a decrease in the amount of rainfall from 1980 to 1990 corresponded with an increase in the expanse of shrubs/herbaceous and grass/herbaceous and, while the amount of rainfall increased for the next five years to 1995, the expanse of shrubs/herbaceous and grass/herbaceous classes reduced correspondingly. From 2000 to 2010, rainfall pattern was up and down and so the extent of grass cover went down and up respectively. There was also a corresponding increase in the expanse of closed savanna class with the amount of rainfall from 1980 to 2000. Also, there appeared to be a similar trend in the pattern of rainfall with the expanse of the closed savanna class, both rising between 1980 and 2000, with the exception that the closed savanna tended to be lagging behind the amount of rainfall for five years. Thereafter, the trend changed and a rise in the amount of rainfall corresponded with a decrease in the expanse of the closed savanna class. The relationships between temperature and the land cover classes were as clear as they were between rainfall and the land cover classes. However, since rainfall time series had an inverse relationship with the temperature time series, it follows

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that temperature affected the land cover classes in the opposite way to rainfall (Figure 24). In general, there appeared to be a trend of change between the amount of rainfall and the expanse of all the land cover classes from 1980 to 1995 and in all cases but the closed savanna class, the trough or peak of the trend occurred in 1990, while trends after 1995 were not consistent.

These trends suggest that the amount of rainfall influenced the open savanna, bare, grass/herbaceous and shrub/herbaceous classes immediately, while the lag phase in the case of the closed savanna was expected for an area that had dense tree cover as it takes longer for trees to respond to changes.

As forecast suggested a relatively low rainfall from 2010 to 2020, the land cover sizes of shrub-land and grassland are expected to reduce and the sizes of closed and open savanna classes are expected to increase correspondingly.

The interclass trends also show some consistent relations was between closed savanna and open savanna and between shrub/herbaceous and grass/herbaceous, and somewhat inverse relations between grass/herbaceous and bare classes (Figure 24). Again, closed savanna lagged behind open savanna but they appeared to show positive relationship. Here, it could be suggested that grass increased at the expense of bare, especially when there was a minimum amount of rainfall; but bare increased at the expense of grass/herbaceous when rainfall increased.

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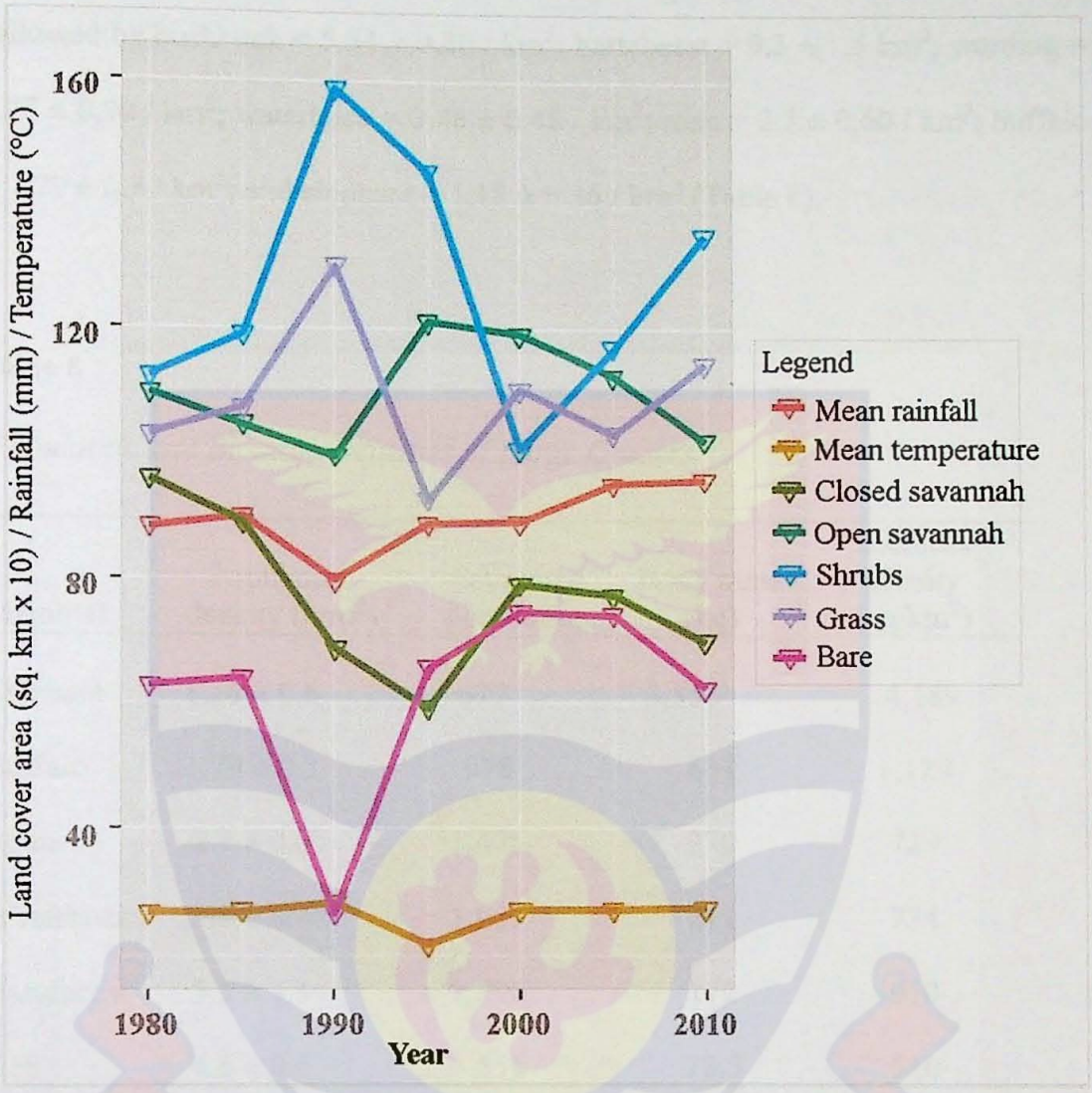


Figure 24: Trend of land cover changes with rainfall and temperature.

Density, Biomass Density and Population Trend

Kob were the most abundant species, reaching the highest estimated population (3,551) followed by bushbuck (2,918) and hartebeest (2,896). The megagrazers (elephant and buffalo) reached 677 and 978 respectively as the lowest populations among the large grazers in the study area (Table 8). In general,

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kob density was the highest, reaching estimated mean density of 6.5 ± 0.60 / km^2, followed by bushbuck = 5.34 ± 0.80 / km^2; hartebeest = 5.3 ± 1.5 km^2; warthog = 4.27 ± 0.90 / km^2; waterbuck = 3.48 ± 0.48 / km^2; roan = 2.7 ± 0.60 / km^2; buffalo = 1.79 ± 0.3 / km^2; and elephant = 1.18 ± 0.36 / km^2 (Table 8).

Table 8

Population and Biomass Densities of Large Grazers

Mammal	Population density (/km^2)	Estimated population	Body mass (kg)	Biomass density (kg/km^2)
Elephant	1.18 ± 0.6	677	3,550	4,189
Buffalo	1.79 ± 0.3	978	631	1,129
Roan	2.7 ± 0.6	1,475	270	729
Waterbuck	3.48 ± 0.48	1,901	211	734
Hartebeest	5.3 ± 1.5	2,896	172	910
Kob	6.5 ± 0.6	3,551	78.5	510
Warthog	4.27 ± 0.9	2,333	73.5	314
Bushbuck	5.34 ± 0.8	2,918	60	320

Population densities of the mammals varied in the different habitat types. In the Anogeissus, BTD and Swamp habitats, kob reached the highest densities of 7.3 ± 1.00 / km^2, 4.78 ± 0.56 / km^2 and 7.8 ± 1.10 / km^2 respectively. In the BTV, hartebeest reached the highest density (10.5 ± 4.30 / km^2) and in the Riverine forest, warthog reached the highest density (Table 9). Elephant and buffalo

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densities were generally low, < 2.0 per sq.km in all habitats except the riverine forest where the elephant attained 5.2 ± 3.5 / km^2 and the Anogeissus where the buffalo reached 6.4 ± 1.80 / km^2 (Table 9). Mammal densities were very high in the riverine forest (Table 9), ranging from 5.2 ± 3.50 / km^2 (elephant) to 24.8 ± 8.70 / km^2 (warthog) and the swamp habitat reached high densities for only waterbuck (6.5 ± 1.10 / km^2), kob (7.8 ± 1.10 / km^2), warthog (5.61 ± 0.86 / km^2) and bushbuck (5.82 ± 0.97 / km^2) (Table 9).

Table 9

Population Densities of Grazers in the Habitat Types

Mammal	Anogeissus	BTD	BTV	Riverine	Swamp
Elephant	0.85 ± 0.19	0.81 ± 0.20	1.39 ± 0.53	5.2 ± 3.50	1.79 ± 0.46
Buffalo	6.4 ± 1.80	1.53 ± 0.31	0.90 ± 0.19	1.08 ± 0.53	1.86 ± 0.66
Roan	1.90 ± 0.37	2.58 ± 0.36	2.8 ± 1.49	8.5 ± 4.30	0.97 ± 0.33
Waterbuck	3.07 ± 0.65	1.55 ± 0.31	3.2 ± 2.20	18.4 ± 4.90	6.5 ± 1.10
Hartebeest	2.66 ± 0.48	2.58 ± 0.39	10.5 ± 4.30	7.1 ± 4.20	1.04 ± 0.38
Kob	7.3 ± 1.00	4.78 ± 0.56	6.7 ± 1.40	12.6 ± 3.30	7.8 ± 1.10
Warthog	5.35 ± 0.85	3.63 ± 0.44	4.8 ± 1.60	24.8 ± 8.70	5.61 ± 0.86
Bushbuck	5.17 ± 0.71	3.14 ± 0.38	6.1 ± 2.30	13.0 ± 4.10	5.82 ± 0.97

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The mammal population densities were also affected by seasonal variation (Table 10). In the dry season, bushbuck reached the highest density (9.3 ± 3.10 / km^2) followed by kob (7.6 ± 1.40 / km^2), waterbuck (6.6 ± 2.90 / km^2) and warthog (6.5 ± 2.10 / km^2), the rest reached relatively very low densities. In the fire season hartebeest reached the highest density (8.1 ± 3.30 / km^2), followed by kob (6.48 ± 0.89 / km^2) with the rest reaching relatively low densities. In the rainy season kob reached the highest density (7.1 ± 1.60 / km^2), followed by warthog (5.67 ± 0.91 / km^2) with the rest reaching relatively low densities; and in the flood season kob reached the highest density (7.7 ± 5.80 / km^2), followed by warthog (6.7 ± 2.70 / km^2) with the rest reaching relatively low densities.

Only about 24% of the study area (and 1.6% of the Park) was sampled by transects and surveyed. The samples were too small in terms of area coverage and the results might not represent a true estimation of the mammal populations. However, considering the total sampling and count efforts used in this study, including a good number of repeated measures, the results are expected to provide good approximations of the population densities and population estimates. It could thus be that apart from the buffalo and the hartebeest, populations of all the large grazers surveyed were higher than previous estimates (Wilson et al., 1993; Mackie, 2004; Bouche, 2006). For example, the elephant population increased from 401 in 2006 to 677 in 2014 and the buffalo population increased from 692 in 2006 to 978 in 2014 (Figure 25). While the increases in the rest of the mammal populations are very interesting, there is skepticism about the 2006 results for being too low. The previous results for the warthog and bushbuck are equally

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unbelievable. But these were results from aerial surveys which were not reconciled by ground surveys (Wilson et al., Bouche, Mackie). Aerial surveys are known to be unsuitable for censusing relatively small mammals like the kob, warthog and bushbuck due to detectability problems. Despite these anomalies, mammalian populations have now improved substantially, 10 years after a heavy loss in 2004 (Figure 25). Most populations have increased beyond the 1993 population maxima. Observed variations in the rate of population growth for the different large grazers were thought to be a result of variation in their responses to environmental changes and differences in recruitment rates.

Total biomass density of the eight large grazers of the MNP was 8,836 kg/km^2. Elephant (4,189 kg/km^2) was the highest, accounting for 53%, followed by buffalo (1,129 kg/km^2; 12%); hartebeest (910 kg/km^2); waterbuck (734kg/km^2); roan antelope (729 kg/km^2); kob (510 kg/km^2); bushbuck (320 kg/km^2); and warthog (314 kg/km^2) (Figure 26). Elephant and buffalo contributed a total of 65% to biomass density with elephant contributing more than 50% while the buffalo contribution is too small for a megagrazer (Figure 26). Though the estimated population for the kob was the highest, this was only 5% of the total biomass of the eight large grazers in the Park. There was no significant relationship between body size and the population density of the mammals ($F(1, 6) = 4.878$, $\rho > 0.05$).

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Table 10

Seasonal Variation in the Population Densities of the Large Grazers

Season	Mammal							
	Elephant	Buffalo	Roan	Hartebeest	Waterbuck	Kob	Warthog	Bushbuck
Dry	2.2 ± 0.70	1.53 ± 0.37	1.42 ± 0.28	6.6 ± 2.90	2.6 ± 1.10	7.6 ± 1.4	6.5 ± 2.1	9.3 ± 3.1
Fire	0.96 ± 0.21	1.66 ± 0.39	2.63 ± 0.85	2.56 ± 0.47	8.1 ± 3.30	6.48 ± 0.89	5.4 ± 1.60	4.8 ± 0.72
Rainy	1.8 ± 1.10	2.89 ± 0.94	2.30 ± 0.47	3.5 ± 1.20	2.71 ± 0.63	7.1 ± 1.60	5.67 ± 0.9	4.8 ± 1.1
Flood	1.76 ± 0.77	1.91 ± 0.65	5.4 ± 3.10	4.8 ± 1.60	7.7 ± 5.80	4.32 ± 0.51	6.7 ± 2.70	3.5 ± 1.0

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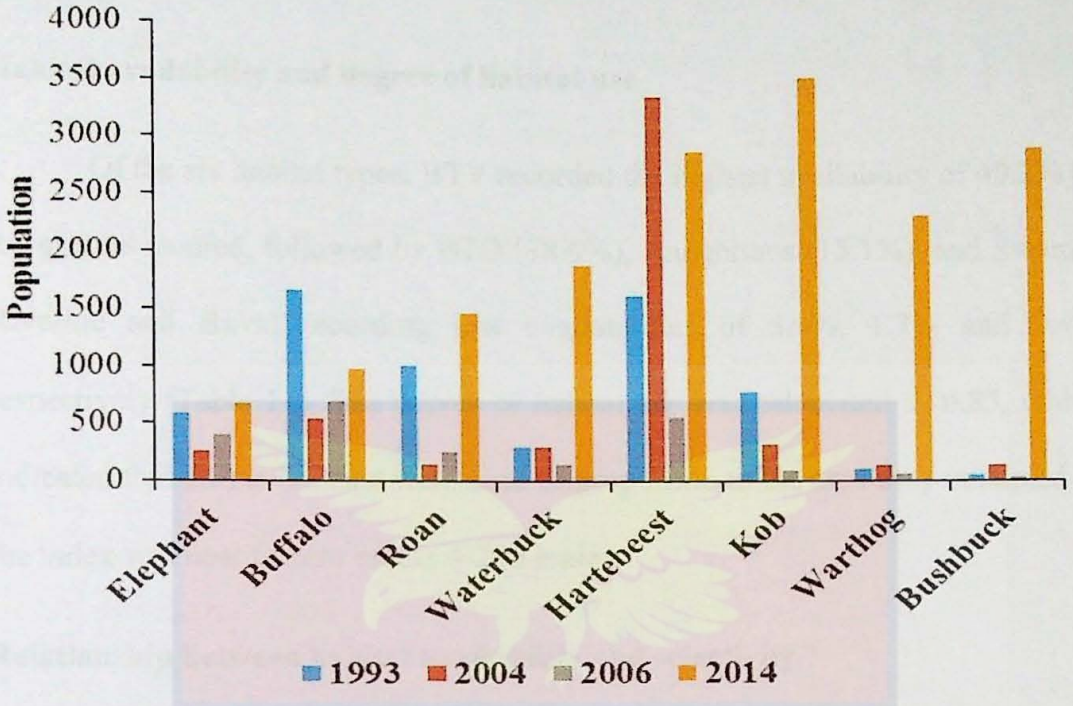


Figure 25: Estimated populations of eight large grazers at MNP.

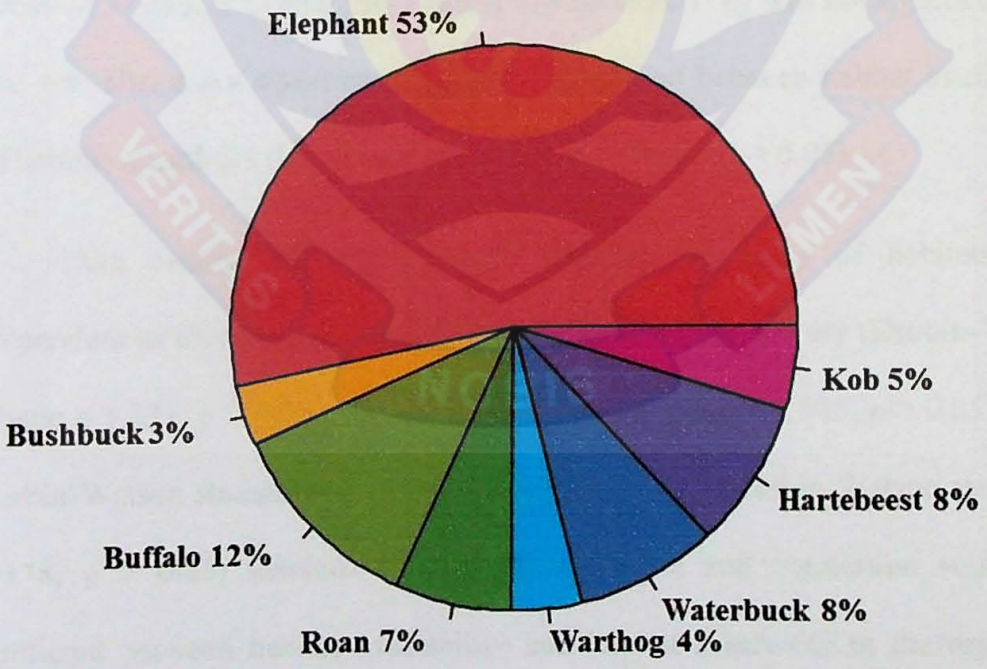


Figure 26: Percentage biomass densities for the large grazers at MNP.

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Habitat Selectivity and Use

Habitat availability and degree of habitat use

Of the six habitat types, BTV recorded the highest availability of 40.2% of the grazers studied, followed by BTD (38.6%), Anogeissus (15.1%), and Swamp, Riverine and Boval recording low availabilities of 3.9%, 1.7% and 0.4% respectively (Table 11). The degree of habitat use was calculated as 0.85, which indicated that all the habitats were used in proportion to the area they occupied as the index was near to zero on the 0-200 scale.

Relationship between habitat availability and selectivity

In general, the Durbin-Watson statistic (2.145) indicated there was no positive autocorrelation ($\rho > 0.05$) in data events for selectivity of habitats. This indicated independence in the data events. Results of ordinary least square regression of habitat availability against habitat selectivity was not significant and there was also a not significant negative correlation between habitat availability and habitat selectivity ($t = -0.469$, $r = -.034$, $R^2 = 0.001$, $\rho > 0.05$).

Data events of large grazers' seasonal selectivity of habitats were independent as there were no positive autocorrelation, in the dry (Durbin-Watson statistic = 1.831; $\rho > 0.05$), fire (Durbin-Watson statistic = 1.985, $\rho > 0.05$), rainy (Durbin-Watson statistic = 2.282; $\rho > 0.05$) and flood (Durbin-Watson statistic = 1.9178, $\rho > 0.05$) seasons. Results of regression and correlation were non-significant between habitat availability and habitat selectivity in the dry ($t = -0.6947$, $r = -.102$, $R^2 = 0.010$, $\rho > 0.05$); fire ($t = -0.228$, $r = -.034$, $R^2 = 0.001$, $\rho >$

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0.05)); rainy ($t = -0.730$, $r = -.106$, $R^2 = 0.011$, $\rho > 0.05$); and flood ($t = 0.658$, $r = .097$, $R^2 = 0.009$, $\rho > 0.05$) seasons. It appeared seasonality did not influence mammal selection of a habitat in relation to the size of habitat available.

Data events for elephant habitat selectivity also showed independence as there was no autocorrelation (Durbin-Watson = 2.166, $\rho > 0.05$) and the t-test by regressing habitat availability against habitat selectivity was also not significant, and so was the correlation between the two variables ($t = -0.721$, $r = -.344$, $R^2 = 0.119$, $\rho > 0.05$). Similar results were observed for buffalo (Durbin-Watson = 2.185, $\rho > 0.05$; $t = 0.991$, $r = .207$, $R^2 = 0.043$, $\rho > 0.05$), roan antelope (Durbin-Watson = 2.071, $\rho > 0.05$; $t = 1.668$, $r = .335$, $R^2 = 0.112$, $\rho > 0.05$); waterbuck (Durbin-Watson = 2.385, $\rho > 0.05$; $t = -1.910$, $r = -.377$, $R^2 = 0.142$, $\rho > 0.05$); kob (Durbin-Watson = 2.421, $\rho > 0.05$; $t = -0.060$, $r = .013$, $R^2 = 0.0001$, $\rho > 0.05$); and bushbuck (Durbin-Watson = 2.335, $\rho > 0.05$; $t = -0.194$, $r = -.041$, $R^2 = 0.002$, $\rho > 0.05$). However, the t-test by regressing habitat availability against habitat selectivity was significant and so was the correlation between the two variables for hartebeest (Durbin-Watson = 2.366, $\rho > 0.05$; $t = 3.383$, $r = .585$, $R^2 = 0.342$, $\rho < 0.01$) and warthog (Durbin-Watson = 2.335, $\rho > 0.05$; $t = -3.066$, $r = -.547$, $R^2 = 0.299$, $\rho < 0.01$). The size of habitat available did not influence habitat use by elephant, buffalo, roan antelope, waterbuck, kob, and bushbuck. The hartebeest showed higher selectivity in larger habitats and smaller selectivity in smaller habitats and warthog, smaller selectivity in larger habitats and higher selectivity in smaller habitats. Only 34.2% and 29.9% of the variation in the

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habitat availability could be explained by variation in habitat selectivity by hartebeest and warthog respectively.

Seasonal variation in habitat selectivity and use

In general, there was very low habitat selectivity by the large grazers, which showed the highest selectivity index (0.118) in the dry season and the lowest (0.003) in the fire season. Selectivity of 0.038 and 0.020 were recorded in the rainy and flood seasons respectively.

There was seasonal variation in the selectivity of habitats by the grazers studied. The five main habitat types, Anogeissus, BTD, BTV, Riverine and Swamp were selected to various degrees seasonally. However, the Boval habitat appeared to be avoided by the buffalo, roan, waterbuck, hartebeest, kob and bushbuck. Only elephant and warthog selected this habitat type. While the elephant selected it, strongly, in the dry and fire seasons but avoided it in the rainy and flood seasons, the warthog avoided the Boval only in the fire season (Table 11).

Elephant and buffalo

Elephant (Figure 27) always selected the swamp habitat only weakly; avoided the Riverine in the dry season but selected the Riverine weakly in the fire and rainy seasons or strongly in the flood season. Elephant also selected the Anogeissus though weakly in all seasons except avoiding it in the dry season; selected the BTD weakly in the dry and rainy seasons but avoided this habitat in the two other seasons; and selected the BTV (weakly) only in the dry and fire

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seasons (Table 11). Buffalo (Figure 28) always selected Anogeissus but only strongly in the dry season and weakly in the fire, rainy and flood seasons; selected the BTD only in the fire season but weakly; selected the BTV only in the flood season; selected the Riverine in the fire and rainy seasons and avoided this habitat in the dry and flood seasons; and used the Swamp in proportion to its availability in the rainy season (Table 11). Thus buffalo preferred the Anogeissus but shifted to the swamp during the rainy season.

Roan antelope, waterbuck and hartebeest

Roan antelope avoided the Anogeissus only in the fire season but selected it (weakly) in other seasons; avoided the BTD in the rainy season but selected the BTD (weakly) in other seasons; weakly selected the BTV in the fire season but avoided the BTV in other seasons; weakly selected the Swamp only in the dry season but avoided it in other seasons; and weakly selected the Riverine in the dry and rainy seasons and avoided this habitat in the other seasons (Table 11). Apart from avoiding the Boval and Swamp all the time with the exception of the dry season when the Swamp was probably dry, roan antelope did not seem to show any clear pattern of habitat selectivity.

Waterbuck always selected Anogeissus, Riverine and Swamp; selection for Anogeissus was weakly, but almost strongly and very strongly for Riverine and Swamp respectively. Waterbuck avoided the other habitats in all seasons (Table 11). Thus waterbuck preferred swampy and riverine habitats to others all the time.

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Hartebeest (Figure 29) selected the BTV (weakly) and avoided the BTD and Boval in all seasons (Table 11). Hartebeest did not seem to have a clear pattern of seasonal habitat selectivity.

Kob, bushbuck and warthog

Kob (Figure 30) selected the Riverine and Swamp in all seasons though weakly; avoided the BTV in all seasons; avoided the BTD in all but the rainy season; and avoided Anogeissus in the dry and rainy seasons and selected it weakly in the fire and flood seasons. It seemed the kob avoided the open plains in the dry and fire seasons when they could be exposed, though they did not show a clear pattern of selectivity for the other habitats.

Bushbuck avoided the Anogeissus only in the fire season and selected this habitat weakly in all other seasons, and weakly selected the BTD only in the fire season; avoided the BTV in all seasons; and selected both Riverine and Swamp weakly in all seasons. It appeared bushbuck preferred swampy and riverine habitats all seasons. Warthog (Figure 31) avoided the Anogeissus only in the fire season and selected it in all other seasons though weakly; weakly selected the BTD only in the rainy season and avoided the BTV in all seasons; weakly selected the Riverine in the flood season but used in proportion to availability in the other seasons; and used the Swamp in proportion to availability in the fire season and weakly in the other seasons (Table 11). Warthog showed preference for the riverine habitat and avoidance of the open plains all season.

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Table 11

Habitat Selection Index for each of the Large Grazers

	Dry season							
Habitat	Elephant	Buffalo	Roan	Waterbuck	Hartebeest	Kob	Bushbuck	Warthog
Anogeissus (15.1%)	-0.22	0.72	0.42	0.04	-0.14	-0.09	0.24	0.24
BTD (38.6%)	0.07	-0.27	0.04	-0.38	-0.07	-0.14	-0.28	-0.44
BTV (40.2%)	-0.21	-0.50	-0.47	-0.26	0.17	-0.03	-0.14	-0.03
Riverine (1.7%)	-0.44	-1	0.39	0.68	0.09	0.50	0.66	0.63
Swamp (3.9%)	0.62	-0.13	0.25	0.77	-0.45	0.47	0.40	0.44
Boval (0.4%)	0.73	-1	-1	-1	-1	-1	-1	0.47

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Table 11, continued

Fire season

Habitat	Elephant	Buffalo	Roan	Waterbuck	Hartebeest	Kob	Bushbuck	Warthog
Anogeissus (15.1%)	0.03	0.51	-0.19	0.25	0.08	0.21	-0.14	-0.18
BTD (38.6%)	-0.50	0.21	0.08	-0.37	-0.04	-0.25	0.10	-0.04
BTV (40.2%)	0.21	-0.70	0.06	-0.47	0.01	-0.01	-0.21	-0.21
Riverine (1.7%)	0.55	0.18	-0.06	0.85	-0.25	0.42	0.53	0.60
Swamp (3.9%)	0.37	-0.07	-0.40	0.62	0.04	0.29	0.35	0.61
Boval (0.4%)	0.73	-1.00	-1.00	-1.00	-1.00	-1.00	-1.00	-1.00

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Table 11, continued

Rainy season

Habitat	Elephant	Buffalo	Roan	Waterbuck	Hartebeest	Kob	Bushbuck	Warthog
Anogeissus (15.1%)	0.05	0.37	0.35	0.06	-0.18	-0.02	0.14	0.18
BTD (38.6%)	0.18	-0.26	-0.04	-0.44	-0.11	0.02	-0.15	0.03
BTV (40.2%)	-0.53	-0.19	-0.21	-0.76	0.23	-0.20	-0.14	-0.39
Riverine (1.7%)	0.67	0.21	0.21	0.88	0.09	0.32	0.33	0.61
Swamp (3.9%)	0.47	0.51	-0.14	0.84	-0.55	0.53	0.53	0.40
Boval (0.4%)	-1.00	-1.00	-1.00	-1.00	-1.00	-1.00	-1.00	0.35

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Table 11, continued

Flood season

Habitat	Elephant	Buffalo	Roan	Waterbuck	Hartebeest	Kob	Bushbuck	Warthog
Anogeissus (15.1%)	0.48	0.44	0.00	0.35	0.24	0.27	0.16	0.19
BTD (38.6%)	-0.26	-0.31	0.39	-0.13	-0.33	-0.04	-0.16	-0.11
BTV (40.2%)	-0.43	0.07	-0.33	-0.70	0.24	-0.28	-0.07	-0.11
Riverine (1.7%)	0.70	-1.00	-0.35	0.81	-0.37	0.44	0.55	0.07
Swamp (3.9%)	0.39	-1.00	-1.00	0.61	-1.00	0.35	0.19	0.30
Boval (0.4%)	-1.00	-1.00	-1.00	-1.00	-1.00	-1.00	-1.00	0.57

(Values ≤ 0 = avoided, > 0 but less than 0.5 = weakly selected, ≥ 0.5 but < 0.7 = used in proportion to availability, ≥ 0.7 but less than 0.9 = strongly selected, and ≥ 0.9 = very strongly selected)

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Figure 27: Elephants in the Mole National Park.

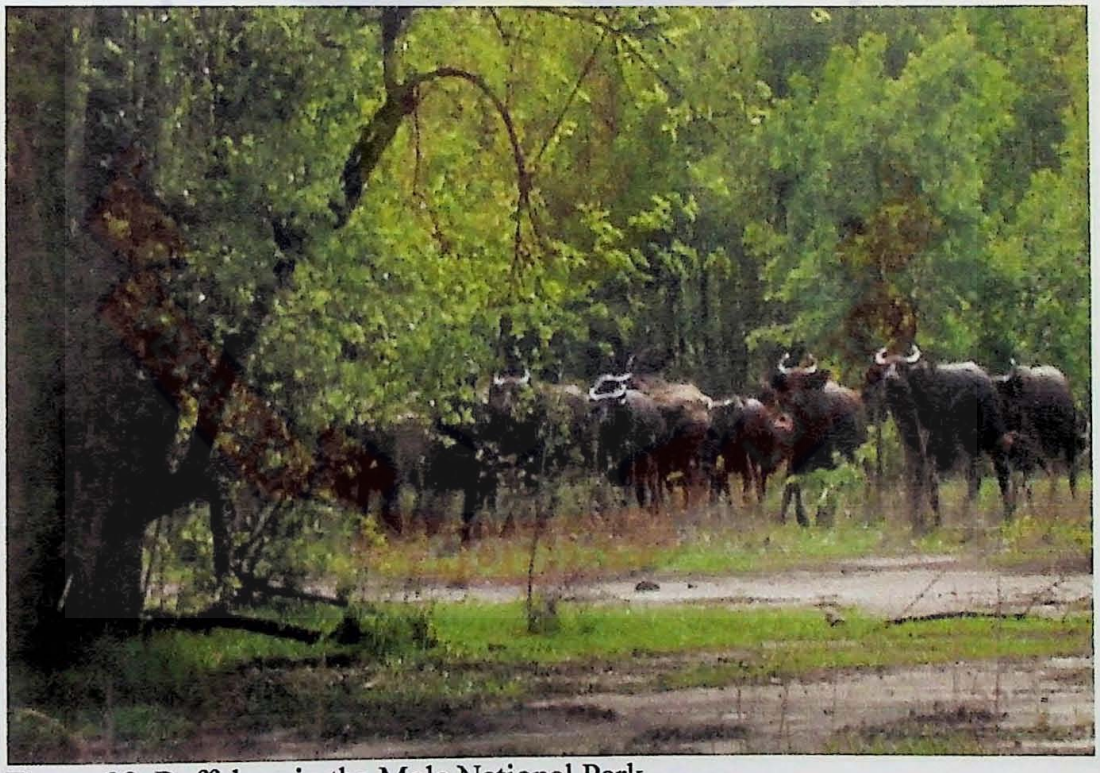


Figure 28: Buffaloes in the Mole National Park.

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Figure 29: A hartebeest in the Mole National Park.



Figure 30: Kobs in the Mole National Park.

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Figure 31: A warthog in the Mole National Park.

Habitat selectivity and body size of mammals

The regression of body mass against habitat selectivity was not significant ($F(1, 190) = 1.278$, $R^2 = 0.007$, $\rho = 0.2597$), and with such a small R^2 value, body size differences did not account for the variation in the proportion of habitat use by a grazer.

The F-ratio for each season was also not significant. For the dry season, $F(1, 46) = 0.217$, $R^2 = 0.004$, $\rho = 0.6439$; fire season, $F(1, 46) = 2.047$, $R^2 = 0.043$, $\rho = 0.1593$; rainy season, $F(1, 46) = 0.010$, $R^2 = 0.0002$, $\rho = 0.9215$, and flood season, $F(1, 46) = 0.0921$, $R^2 = 0.002$, $\rho = 0.7629$.

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Forage Quality and Quantity and Morisita's Overlap of Habitat Use

Seasonal variation in forage quality and quantity

Table 12 shows seasonal variation in the means (and standard errors) of variables representing grass quality (percentage grass greenness, percentage digestible organic matter and percentage crude protein) and grass quantity (grass biomass (kg/m^2) and percentage grass cover). Results of ANOVA indicated a very highly significant seasonal variation in percentage grass greenness ($F(3, 1388) = 113.6$, $\rho < 0.001$) and Tukey's post-hoc analysis indicated very highly significant difference between each pair of dry and rainy seasons ($F = 15.32$, $\rho < 0.001$), dry and flood seasons ($F = 18.59$, $\rho < 0.001$), fire and rainy seasons (17.64, $\rho < 0.001$) and fire and flood seasons ($F = 20.91$, $\rho < 0.001$). However, the difference was not significant between dry and fire seasons, and rainy and flood seasons. Results of ANOVA indicated a very highly significant seasonal variation in percentage crude protein ($F(3, 461) = 6.078$, $\rho < 0.001$) and the difference was very highly significant between fire and rainy seasons ($F = 4.974$, $\rho < 0.01$) and significant between dry and fire seasons ($F = 3.913$, $\rho < 0.05$) and rainy and flood seasons ($F = 4.029$, $\rho < 0.05$) but not significant between dry and rainy seasons, dry and flood seasons, and fire and flood seasons. Results of ANOVA indicated no significant seasonal variation in percentage digestible organic matter. Therefore, it could be that the percentage grass quality was high in the rainy and flood seasons and low in the dry and fire seasons (Table 12).

There was also very highly significant seasonal variation in grass biomass ($F(3, 1388) = 198.2$, $\rho < 0.001$) and Tukey's post-hoc analysis indicated very highly significant difference between each pair of dry and fire seasons ($F = 27.36$,

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$\rho < 0.001$), dry and rainy seasons($F = 14.36$, $\rho < 0.001$), fire and rainy seasons ($F = 13.0$, $\rho < 0.001$), fire and flood seasons ($F = 27.45$, $\rho < 0.001$) and rainy and flood seasons ($F = 14.45$, $\rho < 0.001$); but the difference was not significant between dry and flood seasons. The difference in seasonal variation in percentage grass cover was also very highly significant ($F (3, 1388) = 141.2$, $\rho < 0.001$). Tukey's post-hoc analysis indicated very highly significant differences between each pair of dry and fire seasons ($F = 22.71$, $\rho < 0.001$), dry and rainy seasons ($F = 6.844$, $\rho < 0.001$), fire and rainy seasons ($F = 15.87$, $\rho < 0.001$), fire and flood seasons ($F = 23.4$, $\rho < 0.001$), and rainy and flood seasons ($F = 7.527$, $\rho < 0.001$), but the difference in seasonal variation in percentage grass cover was not significant between dry and flood seasons. Therefore, grass quantity was high in the dry and flood seasons and low in the fire and rainy seasons. Thus, grass (forage) quality and quantity varied seasonally at MNP. In the dry season, as forage quality decreased, forage quantity increased but in the rainy season, forage quality increased and the quantity decreased. Also, the trough of seasonal trend in both forage quality and quantity occured in the fire season and the peak in the flood season (Table 12).

Overlaps of habitat use among the grazers

In general, overlaps between large grazers were low in all seasons. Kob dominated in all seasons with the highest (54%) in the fire season and the lowest (45%) in the rainy season. The lowest overlap by kob was even higher than those of the others in all seasons. The minimum overlap was 6% by buffalo in the flood season. These were thought to reflect the hypothesis that infers that for a low level

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of resource use overlap, competition is not occurring (Jenkins & Wright, 1988). While there was a thin line between low and high overlap in the case of the kob, the grazers, especially buffalo, clearly avoided competition.

Table 12

Means of Variables Representing Grass Quality and Quantity

Variable	Season			
	Dry	Fire	Rainy	Flood
Grass greenness	55.6 ± 1.40	51.3 ± 2.10	84.1 ± 1.60	90.2 ± 1.40
Digestible organic matter	78.8 ± 1.10	75.7 ± 1.20	75.1 ± 1.10	75.9 ± 1.30
Crude protein	7.1 ± 0.10	6.7 ± 0.10	7.3 ± 0.10	6.8 ± 0.10
Grass biomass	0.7 ± 0.01	0.33 ± 0.01	0.5 ± 0.01	0.7 ± 0.01
Grass cover	63.9 ± 1.20	32.05 ± 1.40	54.3 ± 1.40	64.8 ± 1.50

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Overlaps between grazers in each habitat type

Morisita's measure, which is the degree of overlap, C_λ, between grazers in each habitat is presented in Appendix B. In general the degree of habitat overlap by grazers were low (average = 21%; range = C_λ = 0 (no overlap) to C_λ = 60%) and varied between grazers and across habitats. Overlaps were completely absent in the Boval and low in all the other habitat types. In Anogeissus, C_λ ranged from 15% (between hartebeest and bushbuck) to 54% (between kob and bushbuck). In BTD, C_λ ranged from 4% (between roan and warthog) to 60% (between kob and bushbuck). In BTV, C_λ ranged from 1% (between buffalo and waterbuck) to 53% (between hartebeest and roan, and between hartebeest and kob). In the Riverine, C_λ ranged from no overlap (between buffalo and roan) to 42% (between kob and warthog). In the Swamp, C_λ ranged from no overlap (between elephant and buffalo) to 55% (between kob and bushbuck).

Overlap among the grazers also varied seasonally and in general, overlap occurred between each of all the possible pairs of the grazers to some extent with an average of 23% (range = 1-55%. It was highest in the fire season followed by the flood season; but low in the dry and rainy seasons. Elephant (Figure 32), roan antelope (Figure 33), hartebeest (Figure 34), kob (Figure 35) and bushbuck (Figure 36) reached their highest overlaps (at least C_λ = 54%) in the fire season while waterbuck (Figure 37) and warthog (Figure 38) reached their highest overlaps in the flood season (C_λ = 49%). High overlaps in the flood season also occurred between kob and bushbuck (C_λ =50%). In all, buffalo (Figure 39) and waterbuck (Figure 37) overlapped very poorly with all the grazers in all seasons;

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buffalo reached its highest overlap (C_λ =27%) in the flood season with elephant. However, the effect of seasonal variation on the degree of overlap was evident in the other grazers.

Seasonal overlaps between pairs of all the grazers studied in different habitat types were also assessed. In the Anogeissus the frequency of overlap was 97.3% as it occurred between each of 114 pairs of grazers in all seasons except three; two in the dry season and one in the fire season (Table 13). The frequency of overlap was 95.5% in the BTD; 92.9% in the BTV; 62% in the Riverine; 53% in the Swamp; and no overlap (0%) in the Boval in all seasons (Table 13). In the Anogeissus and BTD the minimum frequencies of overlap were 92.9% and 82.1% in the dry and flood seasons respectively. The BTV recorded the same high frequency of overlap (92.9%) each season. The Riverine and Swamp recorded high frequencies of overlap in the fire and rainy seasons and there was no overlap in the swamp in the dry season. While there was completely no overlap in the Boval in all seasons, the frequencies of overlap were always high (at least 75%) in the dry and fire seasons (Table 13) in all other habitat types.

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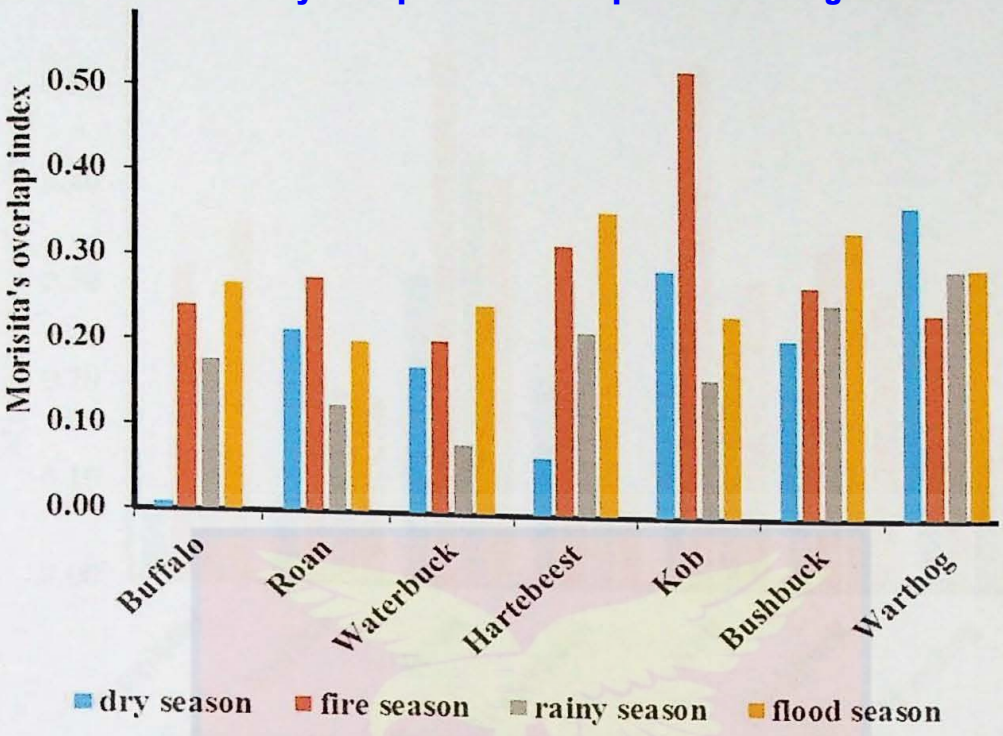


Figure 32: Seasonal variation in Morisita's overlap index between elephant and other grazers.

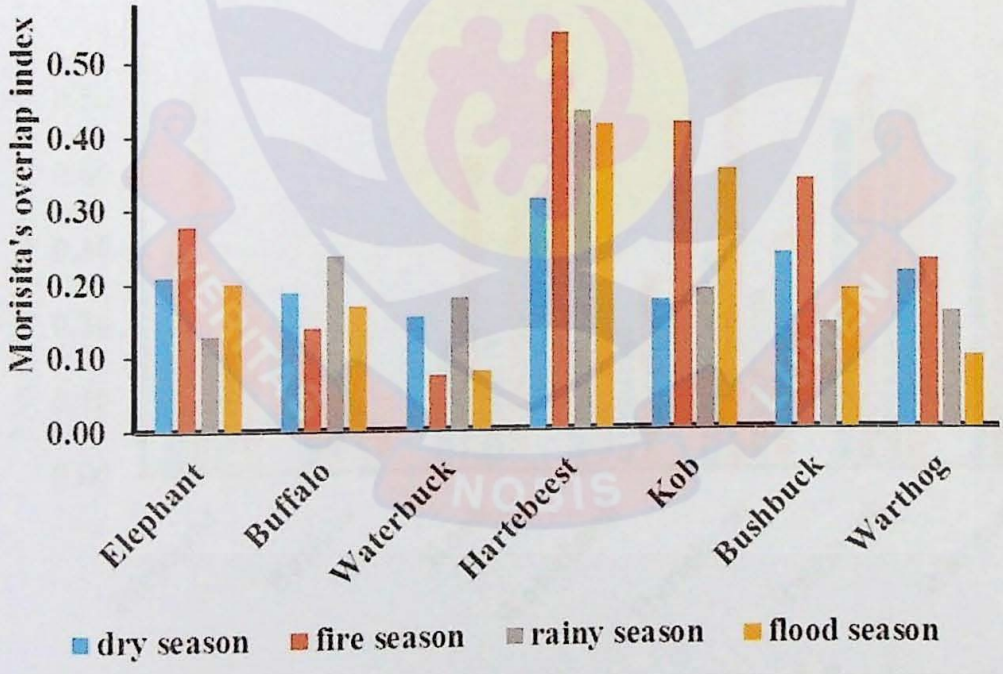


Figure 33: Seasonal variation in Morisita's overlap index between roan antelope and other grazers.

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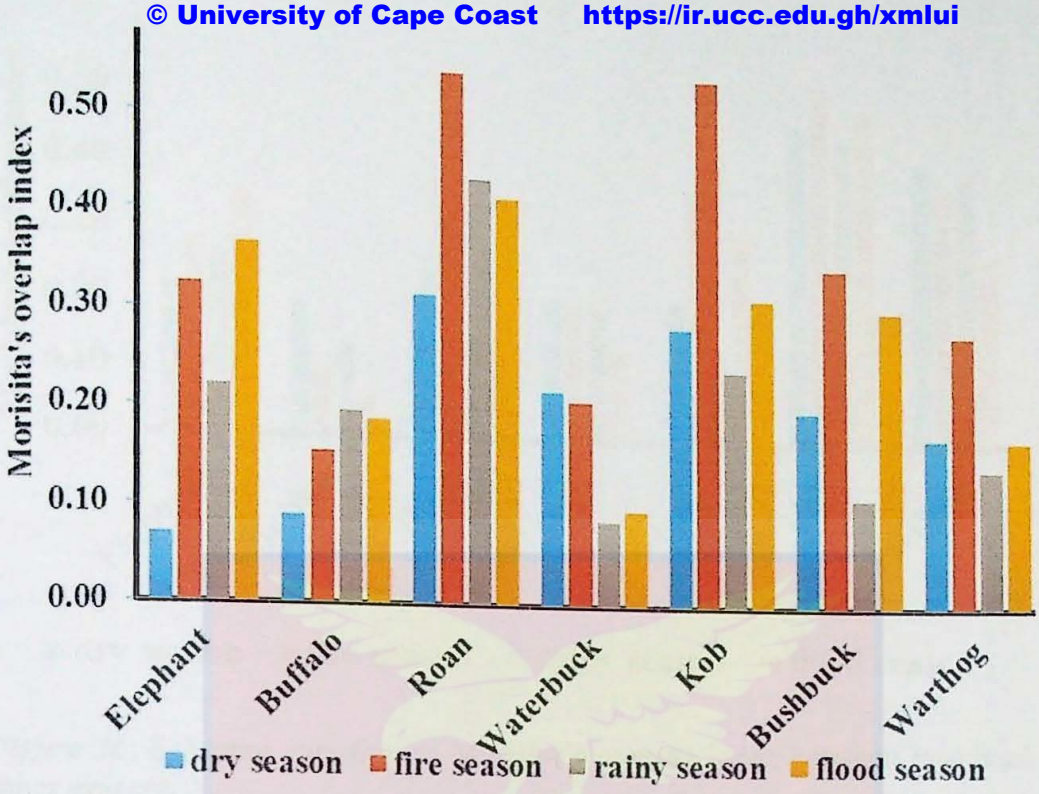


Figure 34: Seasonal variation in Morisita's overlap index between hartebeest and other grazers.

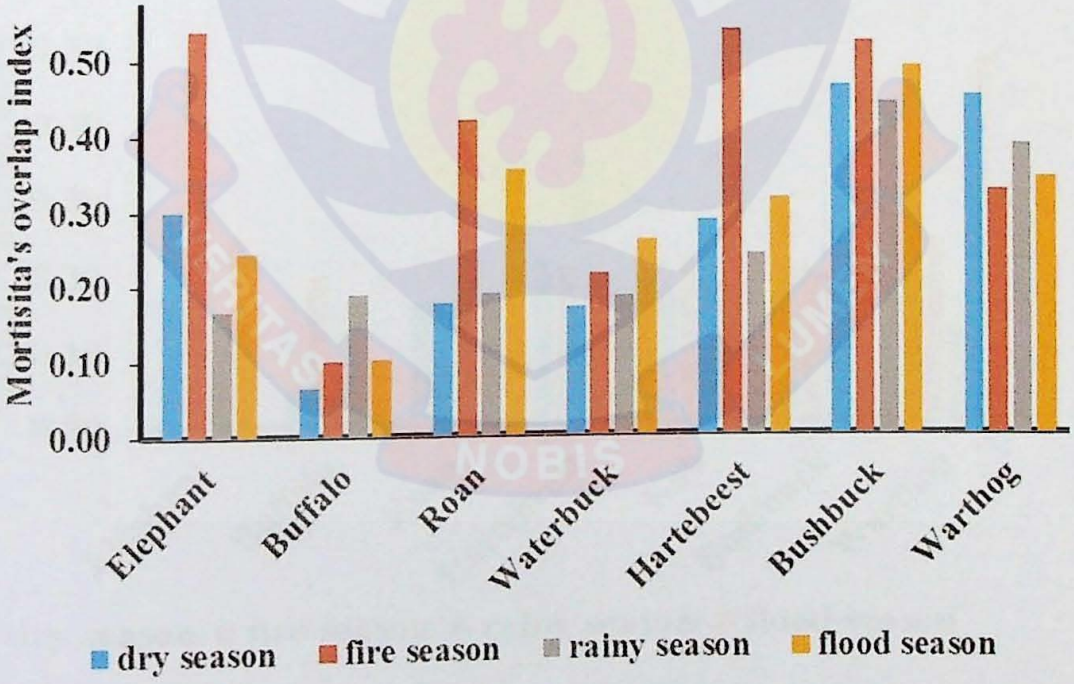


Figure 35: Seasonal variation in Morisita's overlap index between kob and other grazers.

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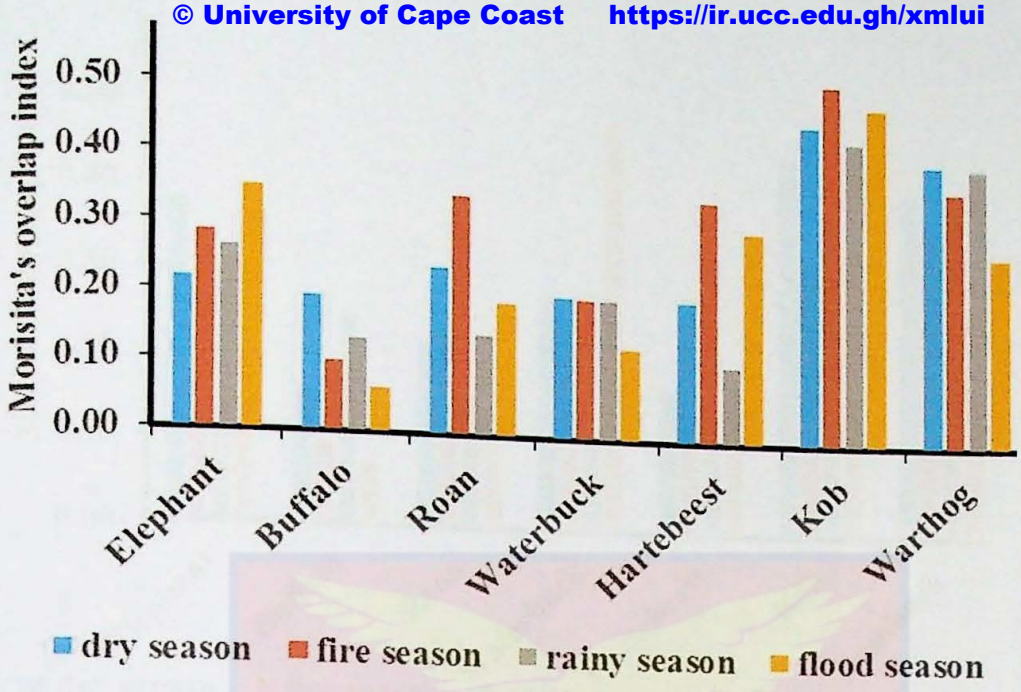


Figure 36: Seasonal variation in Morisita's overlap index between bushbuck and other grazers.

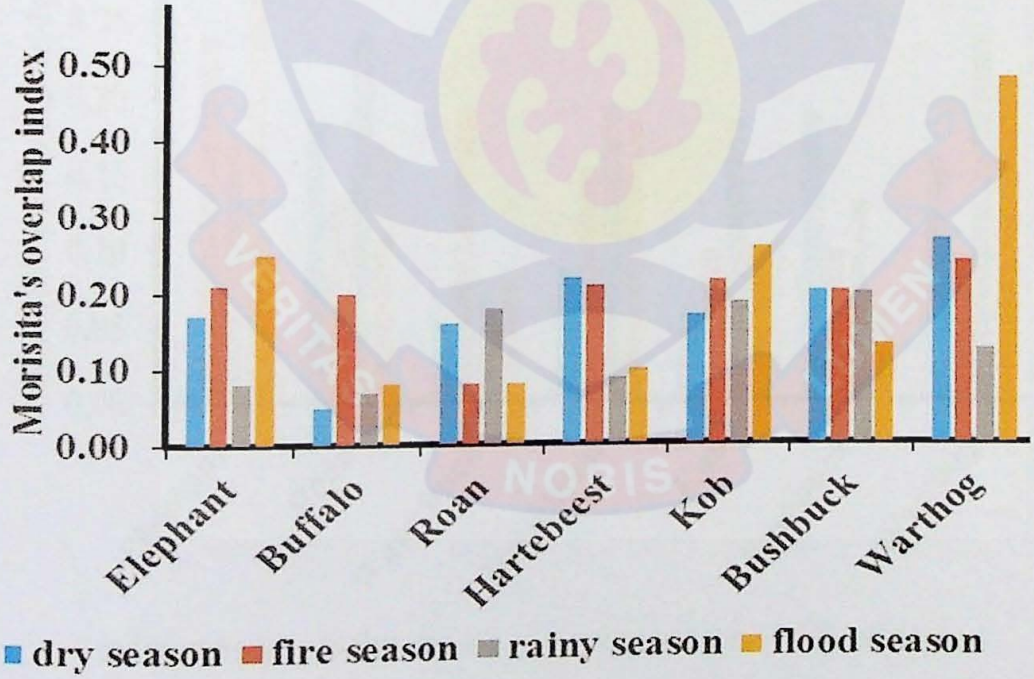


Figure 37: Seasonal variation in Morisita's overlap index between waterbuck and other grazers.

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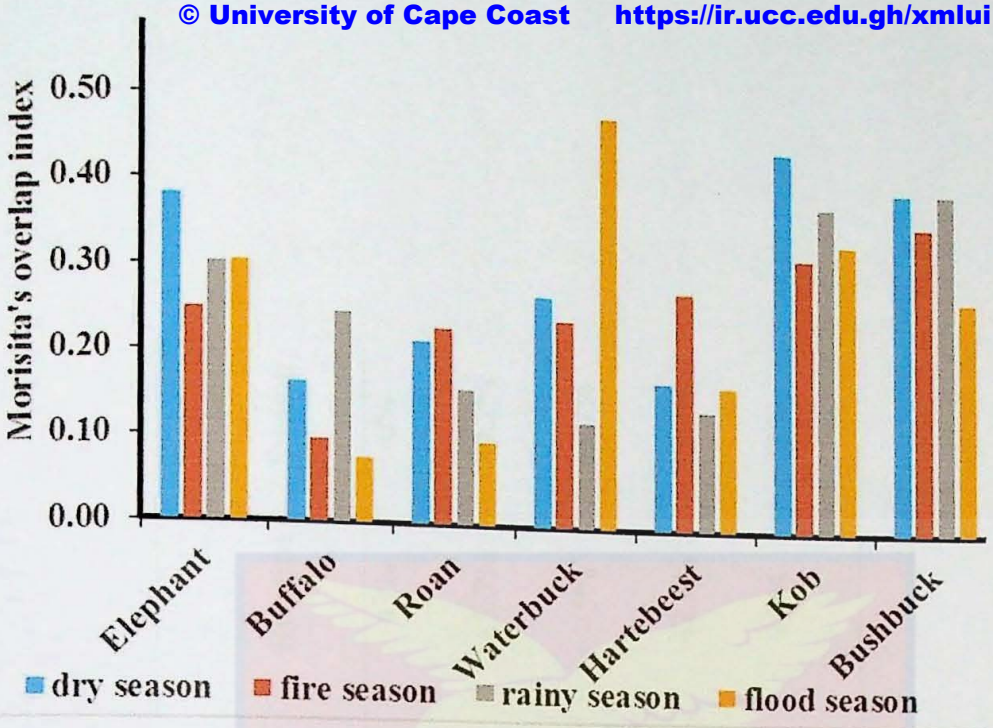


Figure 38: Seasonal variation in Morisita's overlap index between warthog and other grazers.

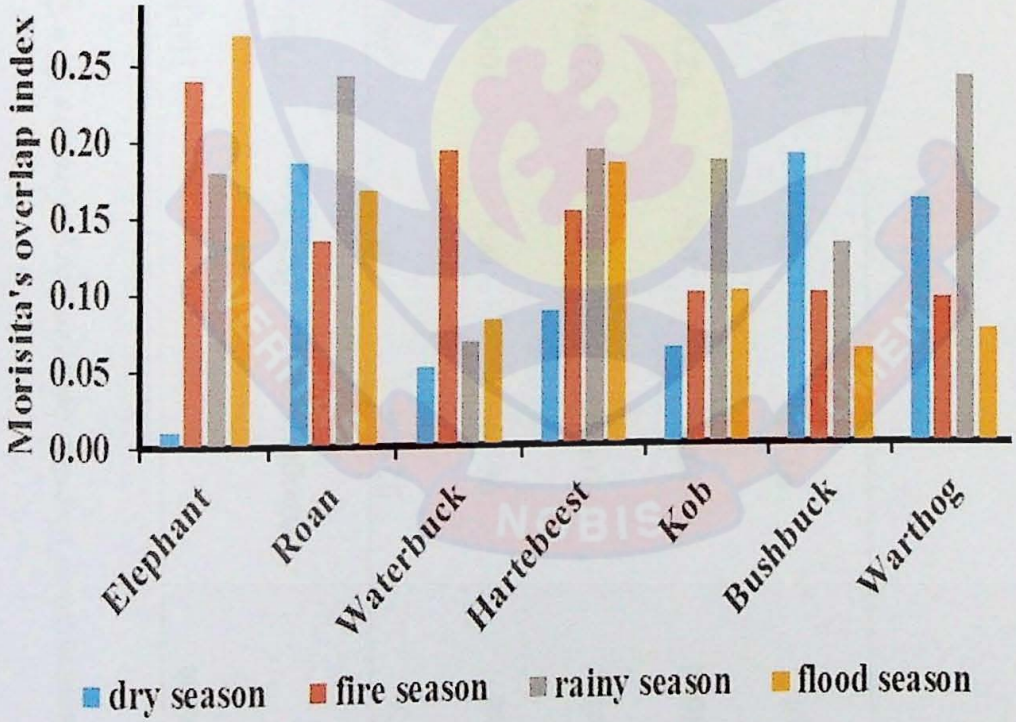


Figure 39: Seasonal variation in Morisita's overlap index between buffalo and other grazers.

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Table 13

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Frequencies of Overlap between Large Grazers (N = 28)

Season	Habitat type					
	Anogeissus	Boval	BTD	BTV	Riverine	Swamp
Dry	92.9%	0%	100%	92.9%	43%	0%
Fire	96.4%	0%	100%	92.9%	85.7%	89.2%
Rainy	100%	0%	92.9%	92.9%	75%	85.7%
Flood	100%	0%	82.1%	92.9%	42.9%	35.7%
All	97.3%	0%	95.5%	92.9%	62%	53%

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Species-Packing

The lists of grazers larger than 2 kg known to occur permanently in MNP (Ghana), Etosha National Park (ENP - Namibia), Hwange National Park (HNP - Zimbabwe), Kafue National Park (KF - Zambia), Kruger National Park (KNP – South Africa) and the Okavango Delta (OD - Botswana) are shown in Table 14. The species richness for MNP was the lowest (21) and KNP reached the highest (33) (Table 15). KF, OD and HNP followed with species richness of 30, 29 and 26 respectively. ENP, about six times the size of MNP, reached species richness of 22, very close to MNP (Table 15). In terms of habitat heterogeneity (diversity), MNP was still the lowest with only six habitat types and again ENP follows with seven habitat types (Table 15). Though HNP is the second smallest Park after MNP it is the most diverse with 19 habitat types (Table 15).

The F-ratio obtained by regressing the natural logarithm of body weight against rank number was very highly significant ($F(1, 19) = 459.9$; $\rho < 0.001$) for MNP. The F-ratio was also very highly significant for each of the other Parks: OD ($F(1, 27) = 458.1$, $\rho < 0.001$); ENP ($F(1, 20) = 491.2$, $\rho < 0.001$); HNP ($F(1, 24) = 427.9$, $\rho < 0.001$); KF ($F(1, 28) = 866.5$, $\rho < 0.001$); and KNP ($F(1, 31) = 1473$, $\rho < 0.001$). Again, with R^2 values ranging from 0.94 to 0.98, the regression model explained 94-98% of the variation in the natural logarithm of body weight. Only 2-6% of the variation in the natural logarithm of body weight could not be explained by its sequence rank. Thus the regression model results in a significantly good degree of prediction; the natural logarithm of body weight of a grazer significantly depends on its rank in the grazer assemblage. Therefore the

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WR (a measure of the degree of species-packing) obtained from the coefficient of the models parameter is reliable. WR of the grazers of the MNP was 1.40, with a total of 21 species. This implied that the average increment in body size between species adjacent in size was 40% (Table 15). MNP had the lowest degree of species-packing (highest WR) and the lowest number of species. The WR of the grazers of ENP followed with a WR of 1.36, with 24 species. The average increment in body size between species adjacent in size was 36%. HNP had a WR of 1.28, with 27 species. OD had 1.25, with a total of 27 species. KF also had a WR of 1.25 with 30 species. KNP had the highest degree of species-packing (1.21) and the highest species richness (33) (Table 15).

A plot of body weight ranks against log body weight (Figure 40) showed that the slope of the regression line for Mole was clearly similar to that of ENP but different from those of HNP, KF, KNP and OD (Table 15). All regression lines shown in Figure 40 are very highly significant ($\rho < 0.001$, all R^2 values > 0.90). The results of a one-way analysis of covariance confirmed very highly significant differences in the slopes of the regression lines between Mole and the five southern Africa conservation areas ($F(1, 5) = 1124$, $\rho < 0.001$). Therefore the degree of species-packing between MNP and the conservation areas in southern Africa are very highly significant. MNP had a very highly significantly lower species-packing (higher WR) than HNP ($T = 4.170$, $\rho < 0.001$), KF ($T = 5.836$, $\rho < 0.001$), KNP ($T = 8.755$, $\rho < 0.001$) and the OD ($T = 6.718$, $\rho < 0.001$). However, the difference in species-packing was not significant between MNP and ENP ($T = 0.054$, $\rho > 0.05$).

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Grazer assemblage structure

Figure 41 shows the distribution of grazers within body weight ranges in the grazer assemblage of the MNP and five other conservation areas in southern Africa. In all cases the highest number of species was found within the 2–50 kg weight range (Figure 41), accounting for nearly half of the total number of species within each assemblage. The ENP, HNP, KF and OD conservation areas had a deficit of species within the 2–50 kg body weight range as compared to MNP, which had slightly more species within that range (Figure 41), and KNP that had exactly half the total number of species. There were generally very low numbers of species within 301–1000 kg weight range; ENP, HNP and MNP had one species each, and KF, KNP and OD had two each within the range. The same two species, hippopotamus and elephant > 1000 kg occurred in all six areas though KNP also had white rhino in this weight range.

Habitat heterogeneity vs species-packing and species richness

Regressing habitat heterogeneity on body weight ratio (species-packing) of the five conservation areas yielded a negative linear relationship (Figure 42), with $R^2 = 0.55$ implying that 55% of the variation in the degree of species-packing in the five conservation areas was explained by variation in habitat heterogeneity. Areas of lower habitat heterogeneity showed a higher body weight ratio (i.e. lower degree of species-packing), while areas with high heterogeneity showed a lower body weight ratio. Regressing habitat heterogeneity against species richness yielded a positive linear relationship. Areas of high habitat heterogeneity supporting high species richness (Figure 43).

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Table 14

List of Large Grazers Occurring in Six Conservation Areas

Species	Scientific name	BW (kg)	ln BW	rank					
				MNP	OD	KF	KNP	ENP	HNP
Whyte's (Togo) hare	*Lepus victoriae*	2	0.693	1		1	1		
Cape hare	*Lepus capensis*	2.2	0.788		1		2	1	1
Egyptian goose	*Alophochen aegyptiacus*	2.3	0.833		2	2	3	2	2
Red rock hare	*Pronolagus randensis*	2.4	0.875				4		
Scrub hare	*L. saxatilis*	2.5	0.916	2	3			3	3
Natal red rock hare	*Pronolagus crassicaudatus*	2.7	0.993				5		
Southern tree hyrax	*Dendrohyrax arboreous*	2.9	1.064			3			
Springhare	*Pedetes capensis*	3.2	1.163		4	4	6	4	4
Rock hyrax	*Procavia capensis*	3.6	1.281	3	5		7	5	
Colobus	*Colobus vellerosus*	4.4	1.482	4					
Cane rat	*Thryonomys gregorianus*	4.8	1.569	5		5			
Green monkey	*Cercopithecus aethiops*	5.2	1.649	6					

(Nomenclature afterKingdon et al., 2013)

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Table 14, continued

Species	Scientific name	BW (kg)	ln BW	rank					
				MNP	OD	KF	KNP	ENP	HNP
Greater cane rat	*Thryonomys swinderianus*	6.8	1.917		7	7	9	7	6
Leopard tortoise	*Gechelone pardalis*	8	2.079		8	8	10	8	7
Sharpe's grysbok	*Raphicerus sharpie*	9.3	2.23			9			
Klipspringer	*Oreotragus oreotragus*	11.9	2.477			10	11		8
Grey duiker	*Sylvicapra grimmia*	12	2.485	7					
Red-flanked duiker	*Cephalophus rufilatus*	13.8	2.625	8					
Oribi	*Ourebia ourebi*	14.1	2.646	9		11	12		
Yellow baboon	*Papio cynocephalus*	19.5	2.97			12			
Grey rhebok	*Kobus vardoni*	20	2.997				13		
Vaal rhebok	*Pelea capreolus*	25.8	3.25				14		
Anubis baboon	*Papio Anubis*	26	3.258	10					
Mountain reedbuck	*Redunca fulvorufula*	29.5	3.384				15		
Chacma baboon	*Papio ursinus*	29.5	3.384		9		16	9	9
Giant pangolin	*Manis gigantea*	33	3.497	11	10				

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Table 14, continued

Species	Scientific name	BW (kg)	ln BW	rank MNP	OD	KF	KNP	ENP	HNP
Springbok	*Antidorcas marsupialis*	39	3.664						
Impala	*Aepyceros melampus*	52.5	3.96		11	13	17	10	10
Common reedbuck	*Redunca arundinum*	58	4.06		12	14	18	11	11
Yellow-back duiker	*Cephalophus silvicultor*	59	4.078	12					
Bush buck	*Tragelaphus scriptus*	60	4.094	13					
Bushpig	*Potamochoerus larvatus*	70	4.248		13	15	19	12	12
Puku	*Kobus vardoni*	71.5	4.27			16			
Warthog	*Phacochoerus aethiopicus*	73.5	4.297	14	14	17	20	13	13
Sitatunga	*Tragelaphus spekei*	76.8	4.341		15	18			14
Kob	*Kobus kob*	78.5	4.363	15					
Nyala	*Tragelaphus angasi*	86	4.454				21		
Kafue lechwe	*Kobus leche*	91	4.511						
Red lechwe	*Kobus leche (kafuensis)*	91	4.511		16	19			15
Tsetsebe	*Damaliscus lulatus*	119	4.779		17		22		16
Ostrich	*Struthio camelus*	120	4.787		18	20	23	14	17
hartebeest	*Alcelaphus buselaphus*	171.7	5.146	16	19	21			

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Table 14, continued

Species	Scientific name	BW (kg)	ln BW	rank					
				MNP	OD	KF	KNP	ENP	HNP
Defassa water buck	*Kobus defassa*	211	5.352	17	20	22	24	15	18.
Oryx	*Oryx gazelle*	225	5.416		21				19
Blue wildebeest	*Connochaetes taurinus*	226	5.421		22	23	25	16	20
Sable	*Hippotragus niger*	227	5.427		23	24	26	17	21
Common zebra	*Equus quagga*	235	5.46		24	25	27	18	22
Roan antelope	*Hippotragus equinus*	270	5.598	18	25	26	28	19	23
Eland	*Taurotragus oryx*	471	6.155		26	27	29	20	
Buffalo	*Syncerus caffer*	631	6.447	19	27	28	30		24
White rhino	*Ceratotherium simum*	1875	7.536				31		
Hippopotamus	*Hippopotamus amphibius*	1900	7.55	20	28	29	32	21	25
Elephant	*Loxodonta africana*	3550	8.175	21	29	30	33	22	26

(Nomenclature afterKingdon et al, 2013)

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Table 15

Regression Slopes and Weight Ratios of Six Different Conservation Areas

Conservation area	Area (km^2)	No. of habitat types	No. of grazer species	Slope	Weight Ratio (WR)	Increment in body weight
Mole National Park	4,840	6	21	0.339	1.4	40%
Etosha National Park	23,175	7	22	0.337	1.36	36%
Hwange National Park	14,621	19	26	0.260	1.28	28%
Kafue National Park	24,000	11	30	0.226	1.25	25%
Kruger National Park	19,633	16	33	0.221	1.21	21%
Okavango Delta	22,000	11	29	0.232	1.25	25%

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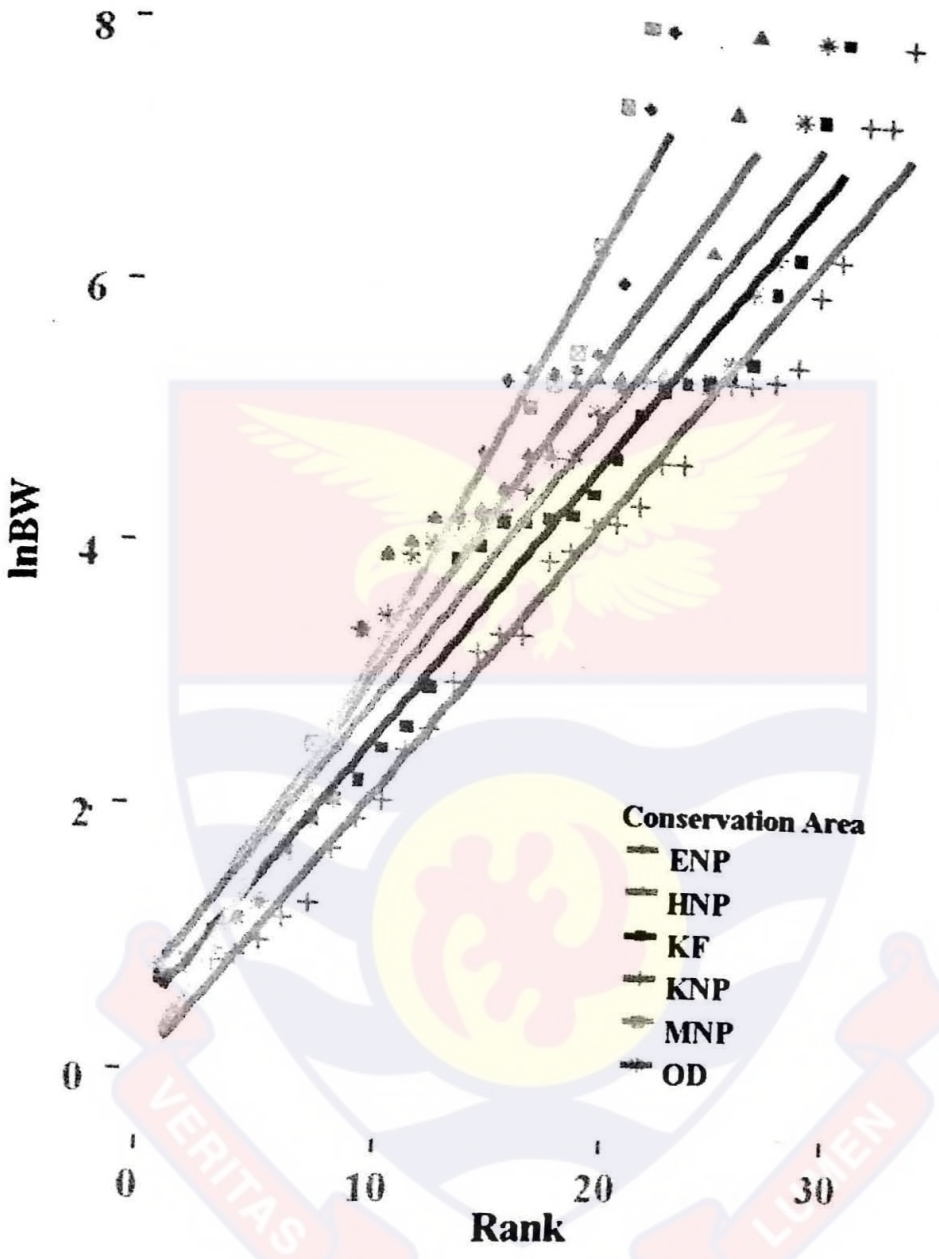


Figure 40: Plot of ln body weight of grazers against their ranked numbers.

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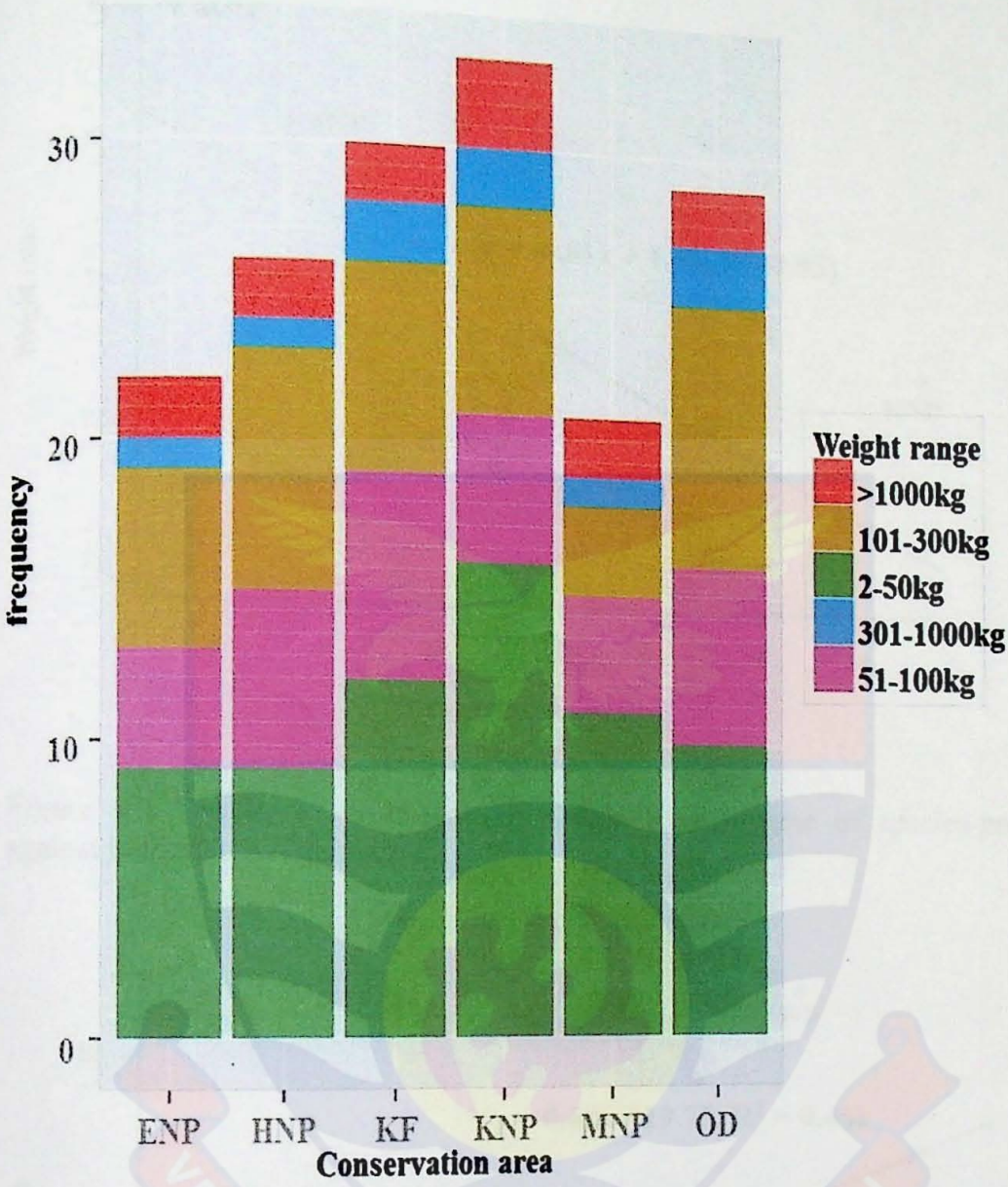


Figure 41: Graphical presentation of weight ranges of large grazers in different conservation areas.

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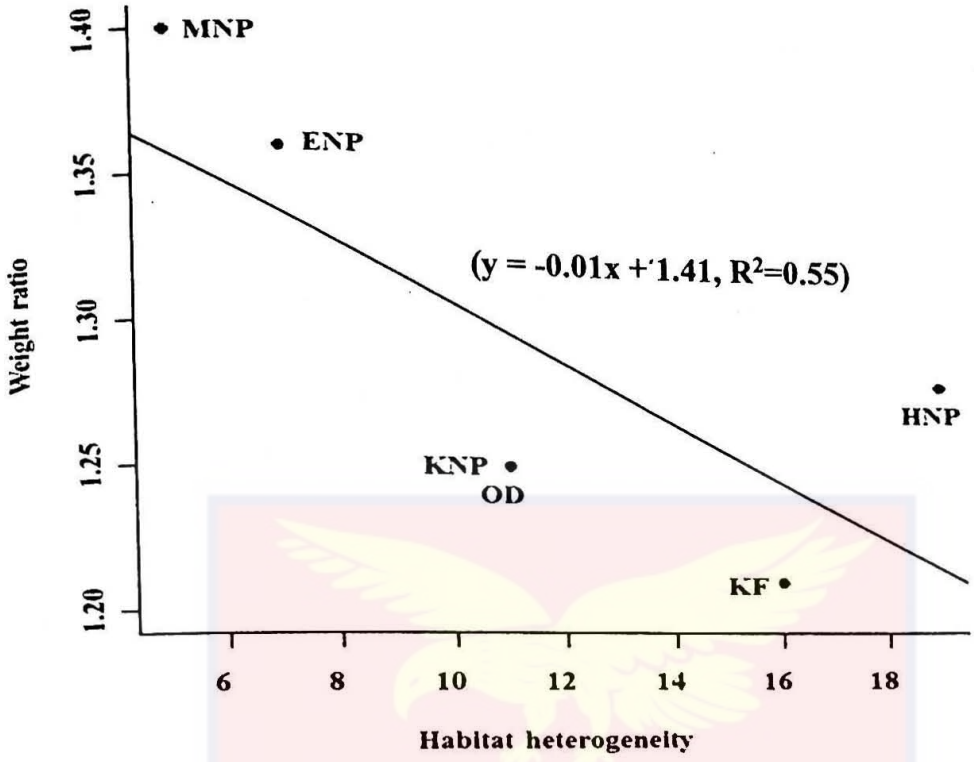


Figure 42: Results of regression of weight ratio (degree of species-packing) against habitat heterogeneity.

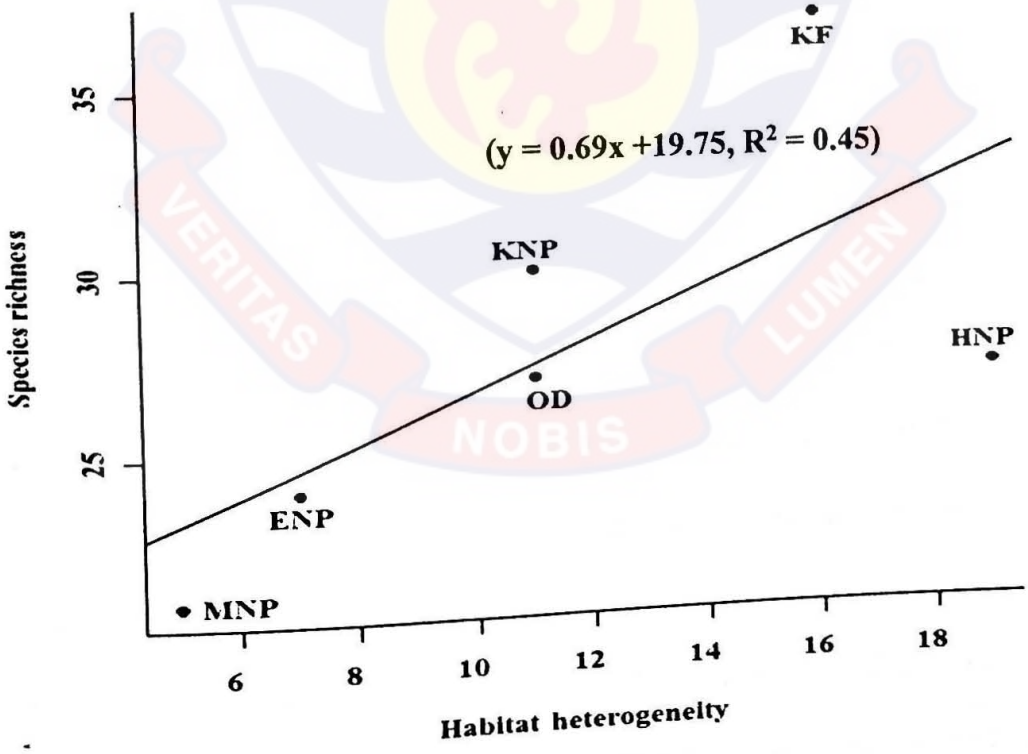


Figure 43: Results of regression of species richness against habitat heterogeneity.

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Effect of Body Size on the Distribution and Abundance of the Large Grazers

There is a steep gradient of body mass variation in the large grazers of MNP (Figure 44) but the F-ratio obtained by regressing body mass of the large grazers against habitat area and the correlation between them were not significant ($F(1, 2507) = 0.446$, $r = -.013$, $\rho > 0.05$) nor were the F-ratio (and correlation) obtained by regressing body mass against percentage greenness ($F(1, 2507) = 1.825$, $r = -.027$, $\rho > 0.05$); grass biomass ($F(1, 2507) = 0.818$, $r = .018$, $\rho > 0.05$); nearest distance to the Park's boundary ($F(1, 2507) = 0.021$, $r = .003$, $\rho > 0.05$); distance to the nearest community ($F(1, 2507) = 3.654$, $r = .038$, $\rho > 0.05$); nearest distance from water ($F(1, 2507) = 0.159$, $r = .008$, $\rho > 0.05$); and altitude ($F(1, 2507) = 0.588$, $r = -.015$, $\rho > 0.05$).

The F-ratio obtained by regressing body mass against each of the variables recorded in the various seasons were also not significant (Appendices C-F). Body size differences did not account for the large grazers' distribution in the MNP.

The F-ratio obtained by regressing body mass against large grazers' abundance was significant ($F(7, 11128) = 38.71$, $\rho < .001$), with $R^2 = 0.024$ implying that only 2.4% of the variation in the abundance of the large grazers could be explained by variation in body size; and with $r = -.034$ suggesting a slight inverse correlation implying that larger grazers are less abundant than relatively smaller ones. Indeed, the relatively small-bodied large grazers (bushbuck, warthog and kob weighing 60–78.5 kg), reached abundance of 1,736–2,461 while the intermediate large-bodied grazers (hartebeest, waterbuck and roan antelope weighing 171.7–270 kg), reached abundance of 1,091–1,648; and the

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megagrazers (buffalo and elephant weighing 631 kg and 3,550 kg respectively) reached abundance of 1,112 and 421, respectively over the period (Table 16). As monthly abundance of the grazers also reflected a similar relationship (Table 16), the results implied that relatively smaller-bodied grazers were more abundant than large-bodied grazers, but the 87.6 % unexplained variance implied that other factors accounted for the abundance of the species more largely.

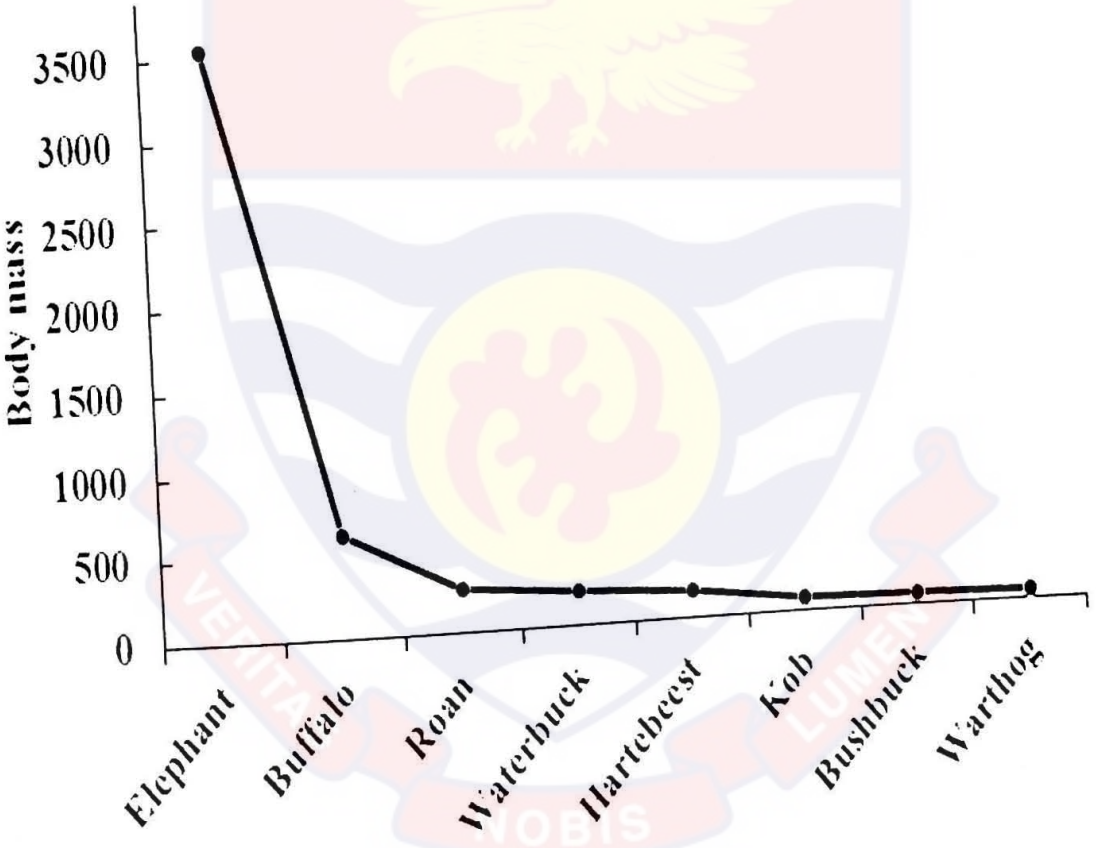


Figure 44: Body mass (kg) variations in the large grazers.

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Table 16

Monthly Abundance of Large Grazers over the Period of Study

Month	Elephant	Buffalo	Roan	Waterbuck	Hartebeest	Kob	Bushbuck	Warthog
September	27	108	115	125	157	218	109	125
October	43	121	70	123	83	190	165	171
November	41	71	76	71	80	250	142	156
December	36	79	67	173	113	180	147	208
January	24	82	89	49	128	210	110	168
February	31	86	100	95	172	188	92	189
March	32	38	187	83	218	196	148	192
April	29	96	104	71	190	244	167	90
May	47	100	111	77	152	165	179	116
June	30	118	116	77	128	234	155	147
July	35	98	85	80	80	220	252	94
August	46	115	80	67	147	166	150	80
Total	421	1,112	1,200	1,091	1,648	2,461	1,816	1,736

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Model fitness and validation

As the data were nested, mixed effect models were ideal for these type of analysis. The final model used in the analysis for each mammal was a good fit, not violating homogeneity (Figures 45-48) or independence. There appeared to be a few outliers but this posed no problems for the mixed effect model analyses. In all analyses for any particular mammal, the standard deviation (a measure of the variability for each random effect-transect, study site and observations added to the model) increased through addition of a random effect. This was to be expected because they were random deviations which resulted from effects not due to transects, study sites or observations. This reflected the fact that each mammal had some factors that affected its distribution that were outside of the purview of this research which were removed, since the random effects, study sites and observations, did not improve the model. It appeared also that in all cases, the different management regimes, study sites or blocks, did not affect the distribution of the mammals significantly, and therefore the same management strategies were in operation and affecting the mammals' distribution the same way in all the study sites. In all cases where *p*–values for the estimates were significant, confidence intervals did not cross zero as expected for the validation of the estimate.

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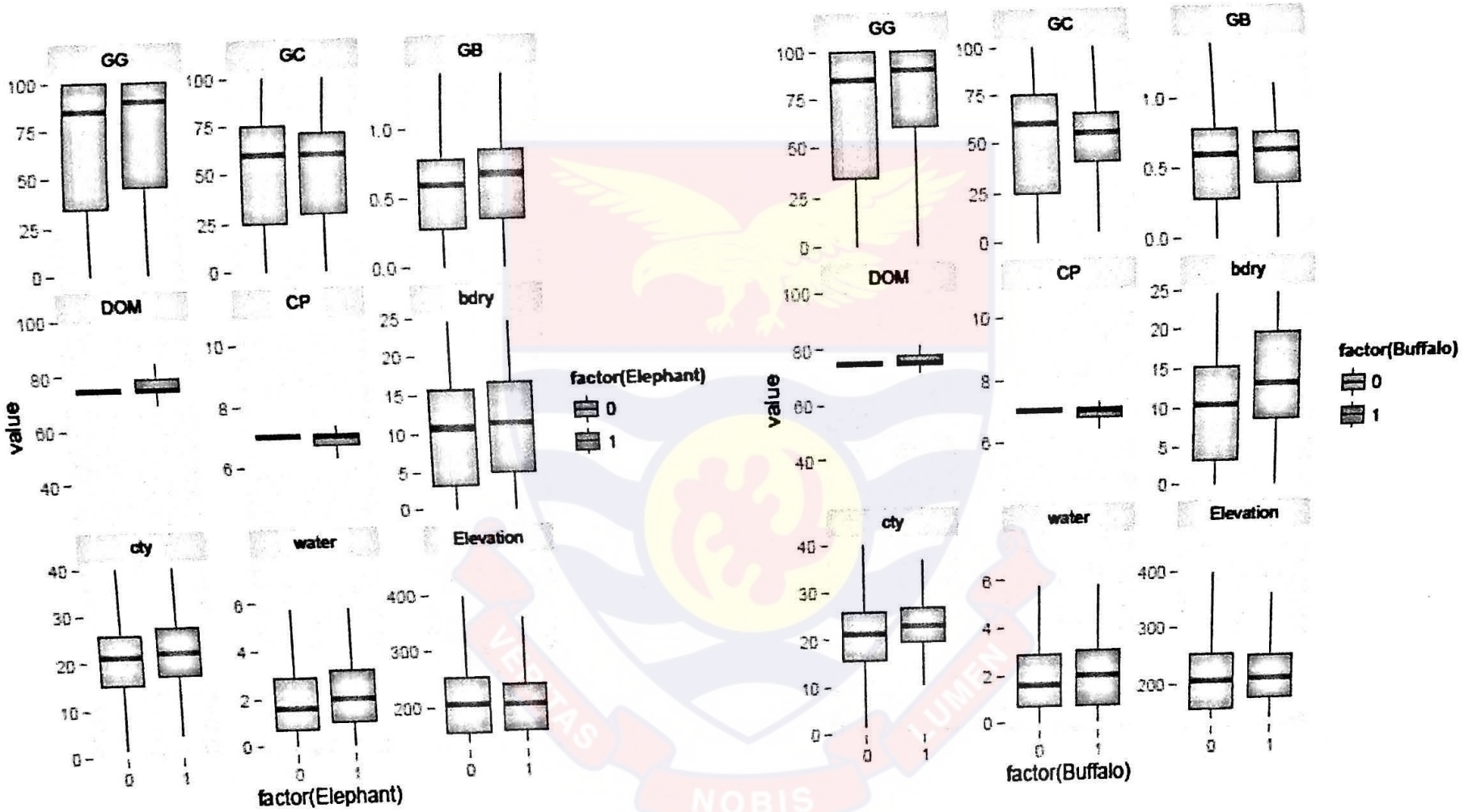


Figure 45: Presence (1) – absence (0) distributions of elephant and buffalo at various values of variables studied at MNP.

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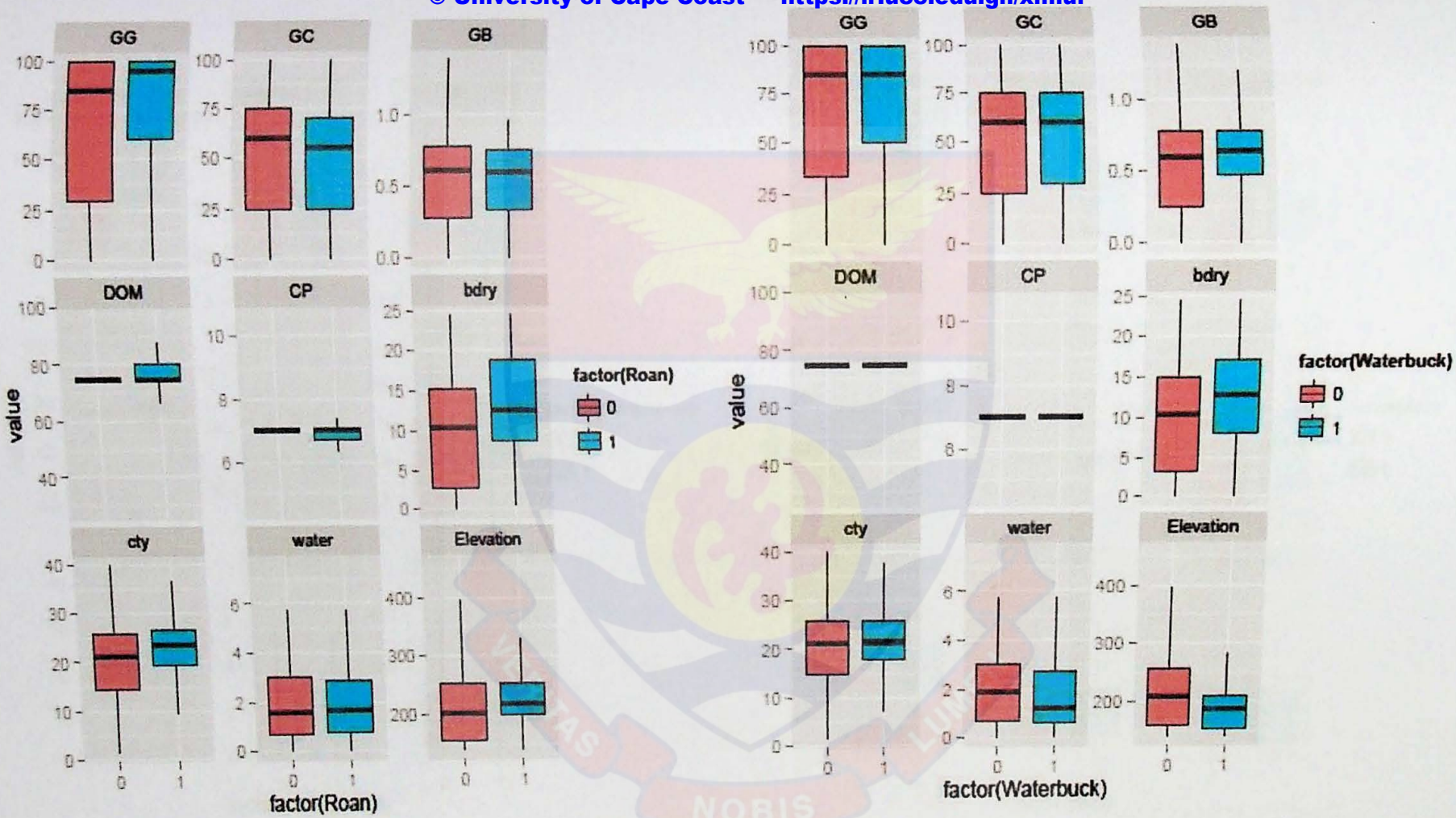


Figure 46: Presence (1) – absence (0) distributions of roan antelope and waterbuck at various values of variables studied at MNP.

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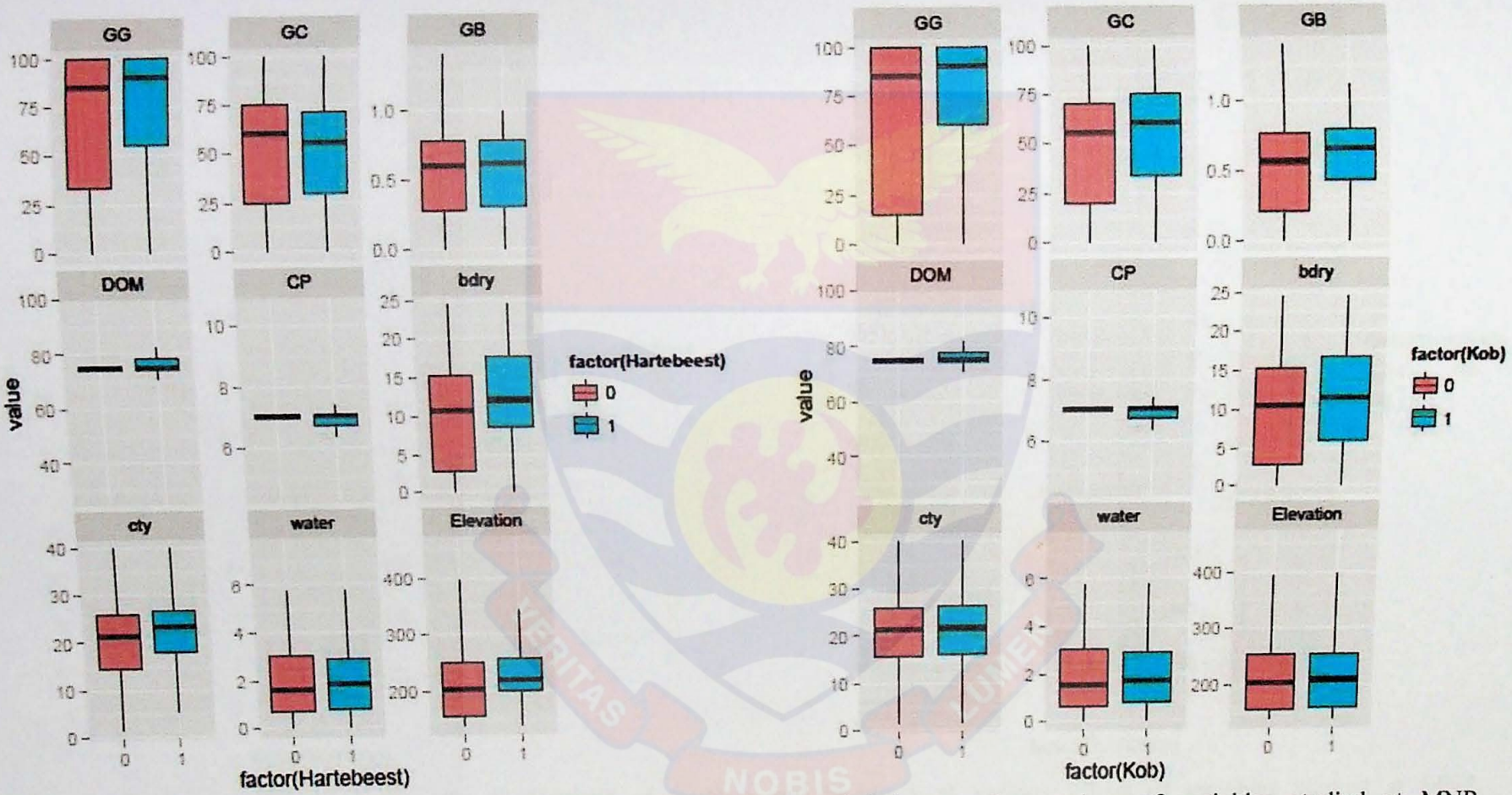


Figure 47: Presence (1) – absence (0) distributions of hartebeest and kob at various values of variables studied at MNP.

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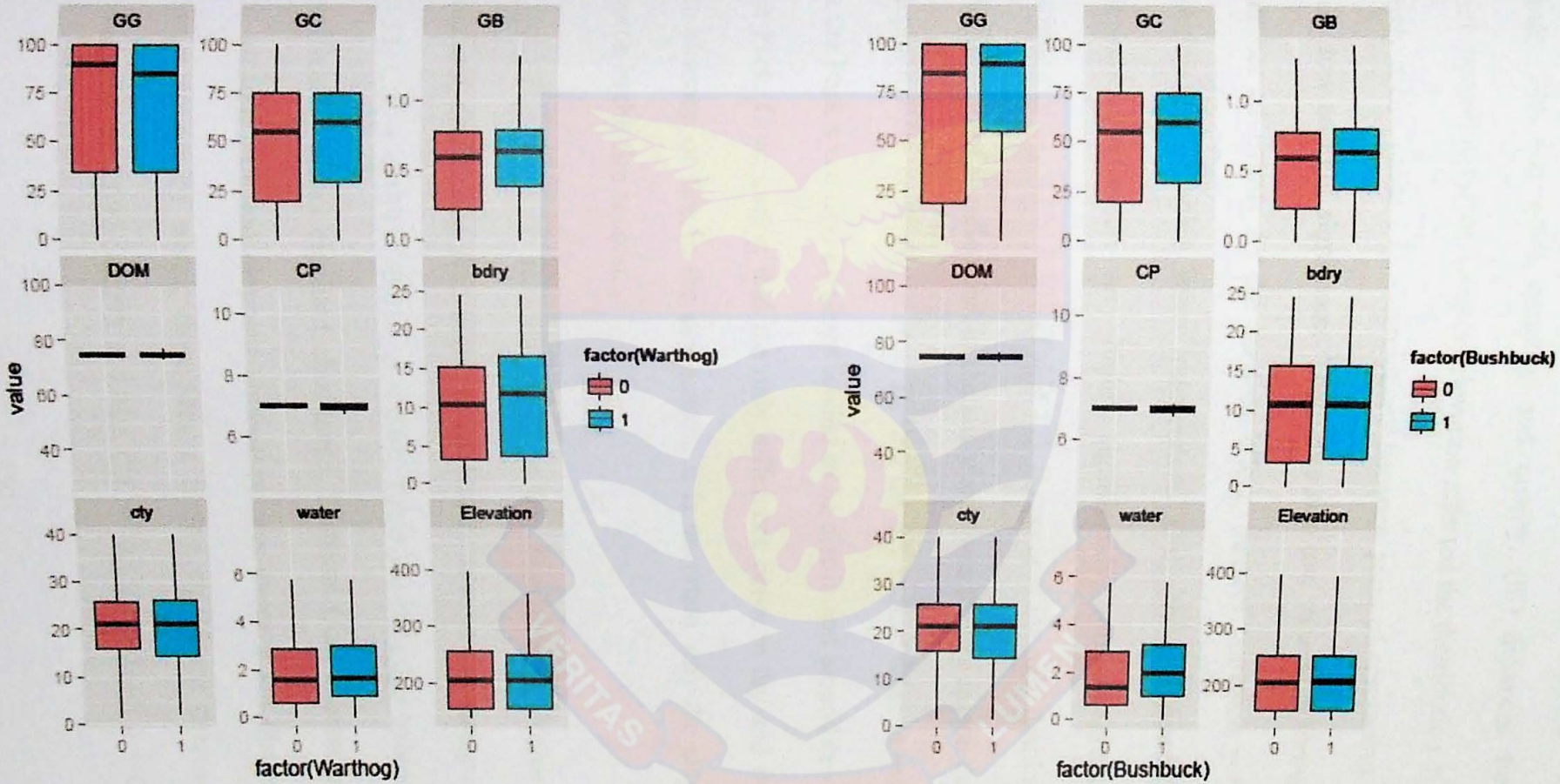


Figure 48: Presence (1) – absence (0) distributions of warthog and bushbuck at various values of variables studied at MNP.

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Elephant distribution and abundance

Apart from seasonality, none of the variables belonging to habitat types (i) study site, (ii) grass quantity and quality, (iii) distances from water, (iv) anthropogenic factors, and (v) elevation affected the distribution of elephant in the study area (Table 17). Correlations between pairs of continuous variables were very low and not significant. There was also low variability throughout the large number of events for the random effect, transect (variance = 0.212) and the continuous variables were independent. Only the dry season predicted the elephant distribution very highly significantly, with a regression coefficient estimate of -4.647 ± 1.308 (Table 17). It appeared the only limiting factor for the distribution of the elephant in the study area was the dry season during which the elephant were generally scarce. During the dry season when streams and rivulets in the Park were dry, elephant tended to be distributed around few water holes in the Park. Considering that the only difference between dry and fire seasons was the absence of fire in the dry season, it is uncertain why the elephant were not scarce in the fire season.

There was no seasonal effect on the abundance of elephant in the MNP. Elephant abundance was highly significantly low in the Anogeissus (-0.386 ± 0.133, C.I. = -0489 – -0.014, $\rho < 0.01$, Table 18) but other habitat types did not significantly affect elephant abundance. Distance from nearest source of water and altitude affected elephant abundance. For every 1 km distance away from nearest source of water, there was a highly significant decrease in elephant abundance by 0.092 (-0.092 ± 0.030, C.I. = -0.150—0.0334, $\rho < 0.01$, Table 18)

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and for every 1 m rise in altitude above sea level, there was a highly significant decrease in elephant abundance by 0.002 (-0.002 ± 0.0009, C.I. = -0.004 – -0.0005, $\rho < 0.01$, Table 18), indicating that elephant tended to be more abundant near sources of water than farther away and at relatively low altitudes than high altitudes.

Table 17

Estimates for Regression Coefficient of Factors Affecting the Distribution of Elephant

Variable	Estimate	Std. Error	z-value	ρ
Dry season	-4.647	1.308	-3.551	0.000***
Fire season	0.180	0.253	0.712	0.476
Flood season	0.099	0.265	0.376	0.707
Rainy season	-0.005	0.252	-0.020	0.984
GG	0.003	0.003	1.005	0.315
GB	0.622	0.342	1.817	0.069
DOM	0.015	0.011	1.292	0.196
CP	0.090	0.110	0.814	0.416
Boundary	-0.002	0.018	-0.137	0.891
Community	0.021	0.016	1.295	0.195
Water	0.072	0.059	1.224	0.221
Altitude	-0.001	0.002	-0.923	0.356

*(*** indicates $\rho < 0.001$)*

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Table 18

Estimates for Regression Coefficient of Factors Affecting the Abundance of Elephant

Variables		Estimate	Std. Error	95% confidence interval		t-value
				LL	UL	
Season	Dry	0.659	0.333	0.006	1.312	1.979
(categorical)	Fire	-0.269	0.108	-0.481	-0.057	-2.491
	Flood	-0.114	0.110	-0.329	0.101	1.040
	Rainy	-0.171	-0.103	0.373	0.031	-1.660
Habitat type	Anogeissus	-0.386	0.133	-0.489	-0.014	-2.895**
(categorical)	Boval	0.486	0.285	-0.072	1.044	1.708
	BTD	-0.201	0.121	-0.438	0.036	-1.661
	BTV	0.022	0.117	-0.208	0.252	0.184
	Riverine	0.362	1.882	-0.007	0.730	1.921
	Swamp	0.178	0.157	-0.129	0.484	1.136
Continuous	GG	0.00002	0.001	-0.002	0.002	0.017
	GB	-0.173	0.159	-0.484	0.138	-1.091
	Boundary	-0.006	0.009	-0.026	0.013	-0.626
	Community	0.0009	0.009	-0.018	0.020	0.094
	Water	-0.092	0.030	-0.150	-0.0334	-3.08**
	Altitude	-0.002	0.0009	-0.004	-0.0005	-2.542**

*(** indicates $\rho < 0.01$)*

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Buffalo distribution and abundance

There was very low variability throughout the large number of events for the random effect, transect (variance = 4.03) and therefore homogeneity was not violated as expected from the model (Figure 49). The distribution of buffalo was affected significantly by both seasonality and habitat types. While effect of dry season was very highly significant (-2.425 ± 0.441, C.I. = -3.289 - -1.561, $\rho < 0.001$) (Table 19), it was not significant in the fire, flood and rainy seasons. Buffalo were scarce during the dry season. Habitat type was also a limiting factor for the distribution of buffalo. There was a very highly significant presence of buffalo in Anogeissus (-2.379 ± 0.401, C.I. = -3.174 – -1.583, $\rho < 0.001$), highly significant presence in BTD (-0.867 ± 0.300, C.I. = -1.456 – -0.279, $\rho < 0.01$), very highly significant presence in BTV (-1.107 ± 0.294, C.I. = -1.682 – -0.531, $\rho < 0.001$), very highly significant presence in Riverine (-1.889 ± 0.526, C.I. = -2.920 – -0.858, $\rho < 0.001$) and very highly significant presence in Swamp (-1.800 ± 0.445, C.I. = -2.673 – -0.927, $\rho < 0.001$) but not in Boval. Buffalo were scarce in all the habitats, despite the wide cover of BTD and BTV (Figure 49). Of all the nine continuous variables investigated, distance from the boundary was the only one that significantly affected the distribution of buffalo (0.066 ± 0.024, C.I. = 0.018 – 0.114, $\rho < 0.01$, Table 19). For every 1 km distance away from the Park's boundary, there was a highly significant increase in the log odds of buffalo presence by 0.066. The buffalo were distributed farther away the Park's boundaries than nearer. Apart from the Boval, the various habitat types occurred

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more extensively near the boundaries of the Park (Figure 49), yet the buffalo were rather distributed far away from the boundaries (Table 19).

Neither did seasonality nor habitat types affect the abundance of buffalo (Table 20). Only nearest sources of water significantly affected the abundance of buffalo -0.202 ± 0.036, C.I. = -0.272 – -0.132, $\rho < 0.001$, Table 20). For every 1 km distance away from the nearest source of water, there was a very highly significant decrease in buffalo abundance by 0.202, indicating that buffalo were more abundant near sources of water than far away.

Table 19

Estimates for Regression Coefficient of Factors Affecting the Distribution of Buffalo

Variables		estimate	Std. error	95% confidence interval		z-value	ρ
				LL	UL		
Season (categorical)	Dry	-2.425	0.441	-3.289	-1.561	-5.502	0.000 (***)
Habitat type (categorical)	Anogeissus	-2.379	0.401	-3.174	-1.583	-5.933	0.000 (***)
	BTD	-0.867	0.300	-1.456	-0.279	-2.891	0.004 (**)
	BTV	-1.107	0.294	-1.682	-0.531	-3.770	0.000 (***)
	Riverine	-1.889	0.526	-2.920	-0.858	-3.592	0.000 (***)
	Swamp	-1.800	0.445	-2.673	-0.927	-4.043	0.000 (***)
-Continuous	Boundary	0.066	0.024	0.018	0.114	2.726	0.003 (**)

*(** indicates $\rho < 0.01$ and *** $\rho < 0.001$)*

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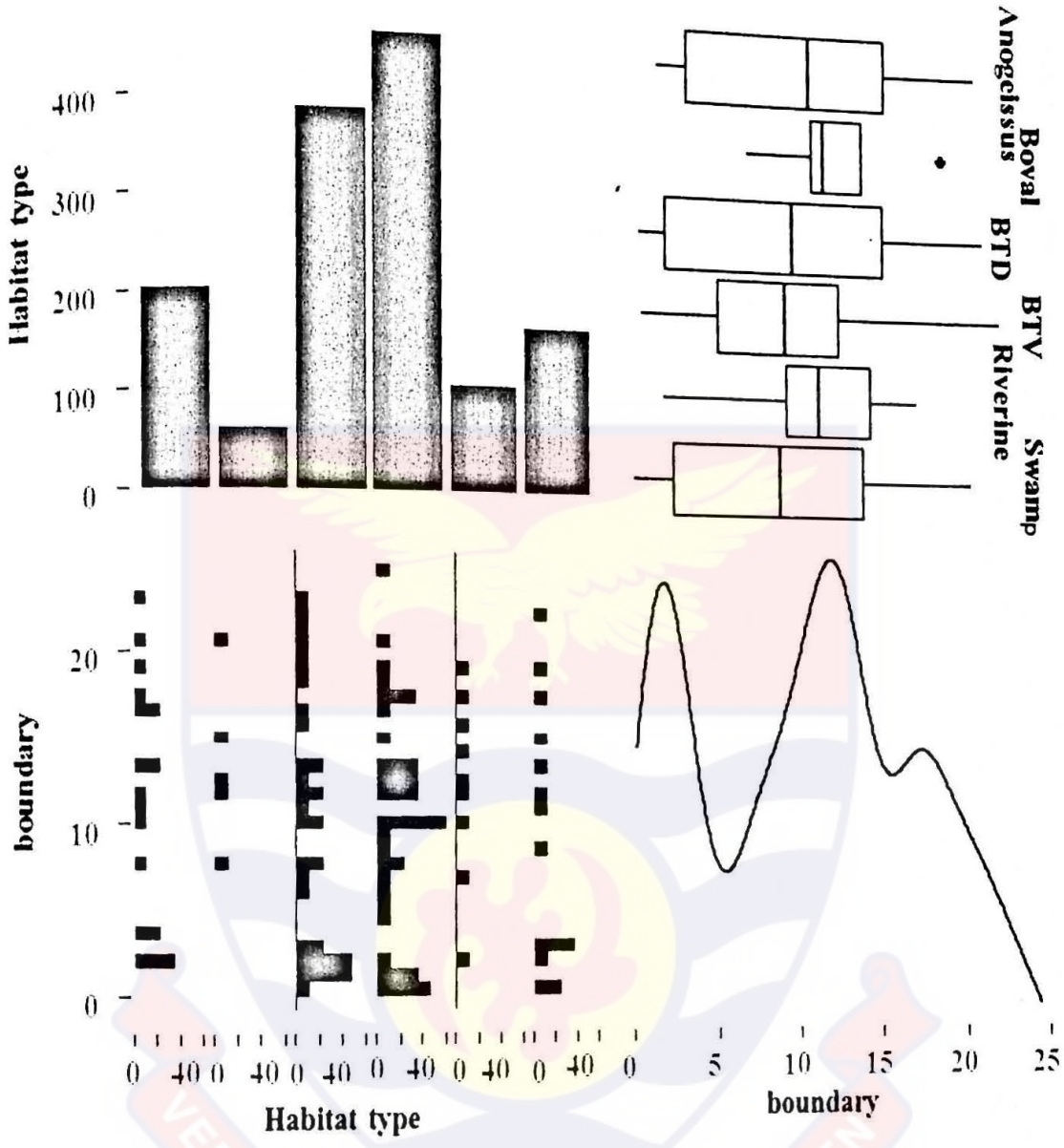


Figure 49: Distributions and relationship between habitat type and distance of buffalo from the Park's boundary.showing kernel density (wiggle in bottom-right panel) for the continuous variable.

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Table 20

Estimates for Regression Coefficient of Factors Affecting the Abundance of Buffalo

Variables		Estimate	Std. Error	95% confidence interval		t-value
				LL	UL	
Season	Dry	1.555	0.532	0.512	2.599	2.921
(categorical)	Fire	-0.062	0.140	-0.336	0.211	-0.448
	Flood	0.231	0.156	-0.075	0.539	1.482
	Rainy	-0.073	0.131	-0.335	0.185	-0.556
Habitat type	Anogeissus	-0.093	0.200	-0.486	0.300	-0.464
(categorical)	BTD	-0.254	0.140	-0.527	0.020	-1.817
	BTV	-0.235	0.135	-0.498	0.029	-1.743
	Riverine	-0.046	0.264	-0.564	0.472	-0.174
	Swamp	0.197	0.227	-0.248	0.643	0.869
Continuous	GG	-0.001	0.002	-0.004	0.003	-0.442
	GB	-0.036	0.225	-0.476	0.404	-0.160
	Boundary	0.0004	0.012	-0.024	0.024	0.035
	Community	-0.024	0.014	-0.052	0.003	-1.722
	Water	-0.202	0.036	-0.272	-0.132	-5.66***
	Altitude	-0.002	0.001	-0.005	0.001	-1.558

*(*** indicates $\rho < 0.001$)*

Roan antelope distribution and abundance

Correlations between pairs of continuous variables, grass greenness, percentage digestible organic matter (DOM) and distance to the community that

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predicted the distribution of roan antelope in the study area were weak (Figure 50). Since there did not seem to be any strong linear relationships among these predictors, the continuous variables were independent.

Seasonality affected the distribution of roan antelope in the study area. The effect of the season was very highly significant in the dry season (-5.564 ± 0.054, C.I. = -5.670 – -5.458, $\rho < 0.001$, Table 21) and fire season (0.257 ± 0.053; C.I. = 0.154 – 0.360, $\rho < 0.001$, Table 21). Roan antelope tended to be scarce during the dry season and common in the fire season. Rainy and flood seasons and habitat types did not affect roan antelope significantly. Habitat shrinkage in the fire season due to burning of vast area of forage contributed to make roan antelope common in the remaining unburnt habitats. Three continuous variables were significant in predicting the distribution of roan antelope: grass greenness (0.009 ± 0.002, C.I. = 0.004 – 0.013, $\rho < 0.001$), DOM- percentage digestible organic matter (0.025 ± 0.006; C.I. = 0.013–0.036; $\rho < 0.001$); and distance to communities (0.049 ± 0.019; C.I. = 0.011–0.086; $\rho < 0.01$, Table 21). For every 1% increase in percentage grass greenness, there was a very highly significant increase in the log odds of roan antelope presence by 0.009. Also, every 1% increase in percentage DOM very highly significantly increased the log odds of roan antelope presence by 0.025 and 1 km distance away from a community highly significantly increased the log odds of roan antelope presence by 0.049. It appears that grass quality was an important predictor of the distribution of roan antelope, which preferred green (fresh) grasses and grasses with higher percentage digestible organic matter. Distance to communities was also a limiting

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factor to the distribution of roan antelope, which were distributed farther away the communities, probably avoiding anthropogenic interference. Kingdon et al. (2013) reported that roan antelope inhabited open or lightly wooded grassland with medium to tall grass and access to water, and avoided areas of short grass, However, none of the variables, habitat types (BTD and BTV in this case) or distance to source of water predicted the distribution of roan antelope in this study. Rather, the dry season appeared an important predictor for the distribution of the roan antelope. In the fire season, it is envisaged that most grasses were burnt.

Both seasonality and habitat types did not significantly affect roan antelope abundance (Table 22). Distance from the nearest source of water and altitude were the only important variables that affected roan antelope abundance. For every 1 km distance away from the nearest source of water, there was a very highly significant decrease in roan antelope abundance by 0.092 (-0.092 ± 0.030, C.I. = -0.150 – -0.0334, $\rho < 0.01$, Table 22), indicating that roan antelope tended to be more abundant near sources of water. Also, for every 1 m rise in altitude above sea level, there was a significant decrease in roan antelope abundance by 0.002 (-0.002 ± 0.0009, C.I. = -0.004 – -0.0005, $\rho < 0.01$, Table 22), indicating that roan antelope tended to be more abundant at relatively low altitudes than high altitudes.

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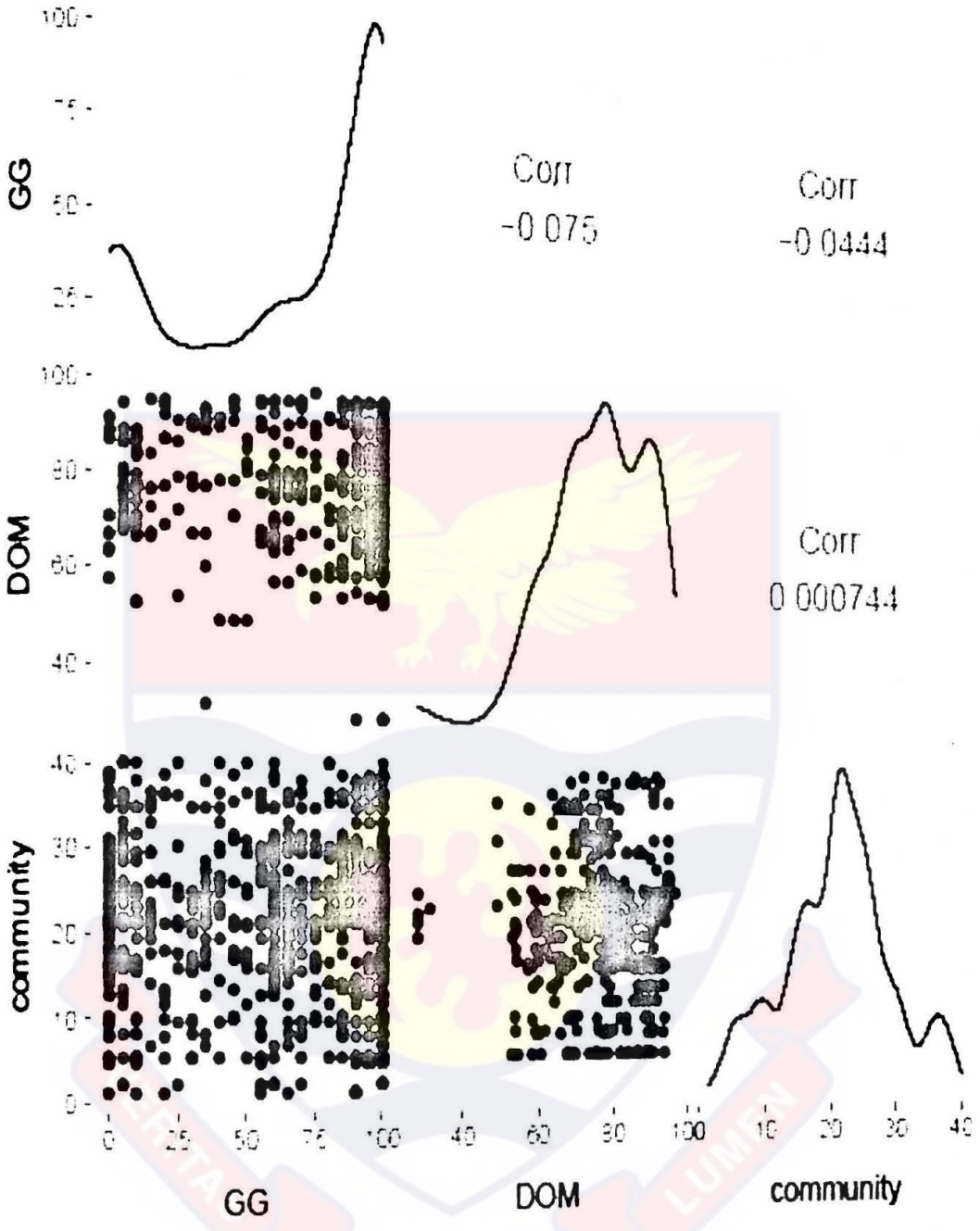


Figure 50: Panels showing distributions of continuous variables from the model predicting roan antelope spatial distribution, correlations between pairs of continuous variables and kernel densities (diagonal wiggles).

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Table 21

Estimates for Regression Coefficient of Factors Affecting the Distribution of Roan Antelope

Variables		Estimate	Std. Error	95% confidence interval		z-value	ρ
				LL	UL		
Season (categorical)	Dry	-5.564	0.054	-5.670	-5.458	-103.09	0.000 (***)
	Fire	0.257	0.053	0.154	0.360	4.87	0.000 (***)
	Flood	-0.105	0.054	-0.211	0.0004	-1.95	0.051
	Rainy	0.085	0.054	-0.022	0.192	1.56	0.118
Continuous	GG	0.009	0.002	0.004	0.013	3.74	0.000 (***)
	DOM	0.025	0.006	0.013	0.036	4.29	0.000 (***)
	Community	0.049	0.019	0.011	0.086	2.58	0.010 (**)

*(** indicates ρ < 0.01 and *** ρ < 0.001)*

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Table 22

Estimates for Regression Coefficient of Factors Affecting the Abundance of Roan Antelope

Variables		Estimate	Std. Error	95% confidence interval		t-value
				LL	UL	
Continuous	GG	0.001	0.002	-0.003	0.004	0.372
	GB	0.141	0.216	-0.283	0.565	0.652
	Boundary	-0.007	0.013	-0.034	0.019	-0.536
	Community	0.009	0.013	-0.016	0.034	0.705
	Water	-0.178	0.035	-0.247	-0.109	-5.03 (***)
	Altitude	-0.003	0.001	-0.005	-0.0004	-2.288 (*)

(indicates $\rho < 0.05$ and *** $\rho < 0.001$)*

Waterbuck distribution and abundance

There was very low variability throughout the large number of events for the random effect, transect (variance = 4.03). Figure 51 shows independence of each continuous variable as correlation between them was very weak, and also suggests availability of less grass quantity at altitudes above 350 m and grass biomass more than 1 kg/m^2 was very rare in MNP.

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The distribution of waterbuck was predicted significantly by habitat types but not seasonality. The distribution of waterbuck was significant in BTD (-0.548 ± 0.250, C.I. = -1.038 – -0.057, $\rho < 0.05$, Table 23), very highly significant in BTV (-1.112 ± 0.256, C.I. = -1.614 – -0.610, $\rho < 0.001$, Table 23) and highly significant in Riverine (0.812 ± 0.308, C.I. = 0.208 – 1.416, $\rho < 0.01$, Table 23) but not significant in Anogeissus, Boval or Swamp. While the waterbuck were very scarce in the BTD, it was common in the BTV and Riverine habitat types. Grass quantity (grass biomass) predicted the distribution of the waterbuck significantly (0.659 ± 0.280, C.I. = 0.109 – 1.208, $\rho < 0.05$, Table 23); altitude also predicted their distribution significantly (-0.004 ± 0.002, C.I. = -0.008 – -0.0002, $\rho < 0.05$, Table 27).

For every 1 kg/m^2 increase in grass biomass, there was a significant increase in the log odds of waterbuck presence by 0.659, and for every 1 m rise in altitude above sea level there was a significant decrease in the log odds of waterbuck presence by 0.004. Waterbuck tended to inhabit places in the low lands, particularly in the Riverine, which give them large quantities of grass to eat. This is consistent with reports by Kingdon et al. (2013) that the habitats of the waterbuck are mainly savanna woodlands and forest-savanna mosaics near permanent water. However, as permanent water all year round was available in only few water holes in few transects in the study area, and most water bodies were ephemeral, it was to be expected that the relationship between waterbuck distribution and water sources was not significant. Though this makes interpretation of the effect of water on the distribution of waterbuck difficult, it is

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envisaged that the waterbuck inhabited lowlands to be near to water; but they also preferred dry ground as reported by Estes (1991). Waterbuck were classified as grazers, but also browse (Estes, 1991) and therefore a combination of BTV and riverine forest, which provide grasses and browses altogether, were ideal habitats for the waterbuck in MNP.

Seasonality did not significantly affect the waterbuck abundance and while five of the habitat types did not significantly influence the waterbuck abundance, there was a very highly significantly low abundance in the BTD (-0.267 ± 0.126, C.I. = -0.513 – -0.021, $\rho < 0.001$, Table 24). Distance from nearest source of water and altitude were also important variables that affected waterbuck abundance. For every 1 km distance away from nearest source of water, there was a very highly significant decrease in waterbuck abundance by 0.193 (-0.193 ± 0.036, C.I. = 0.264 – -0.122, $\rho < 0.001$, Table 24). For every 1 m rise in altitude above sea level, there was a significant decrease in waterbuck abundance by 0.002 (-0.002 ± 0.0009, C.I. = -0.004 – -0.0001, $\rho < 0.05$, Table 24). Waterbuck tended to be more abundant near sources of water than farther away and at relatively low altitudes than high altitudes.

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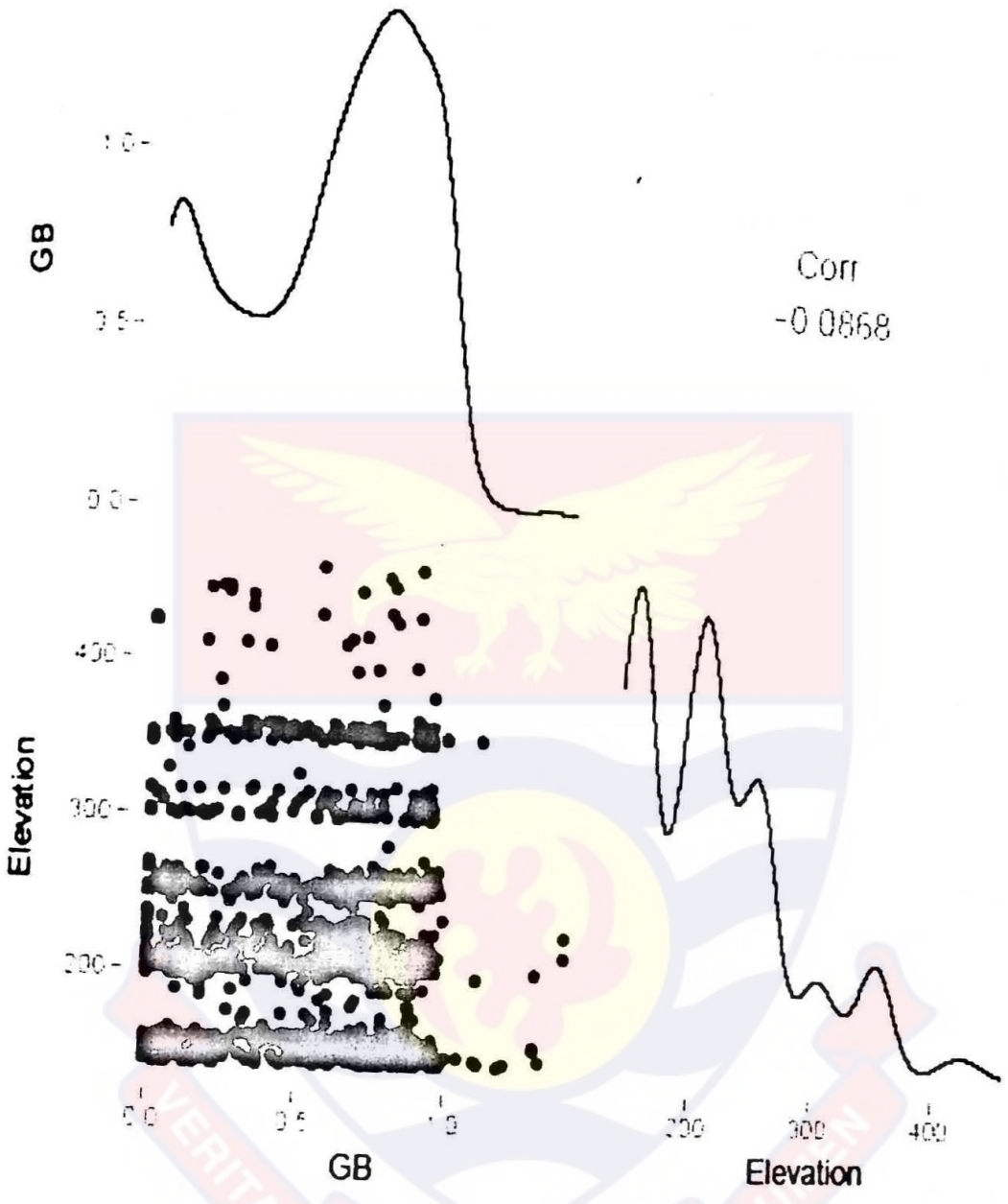


Figure 51: Panels showing distributions of continuous variables from the model predicting waterbuck spatial distribution, correlations between continuous variables and kernel densities (diagonal wiggles).

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Table 23

Estimates for Regression Coefficient of Factors Affecting the Distribution of Waterbuck

Variable		estimate	std. error	95% confidence interval LL	UL	t-value
Habitat type (categorical)	Anogeissus	-0.240	0.128	-0.490	0.011	-1.873
	BTD	-0.267	0.126	-0.513	-0.021	-2.12***
Continuous	Water	-0.193	0.036	-0.264	-0.122	-5.31***
	Altitude	-0.002	0.0009	-0.004	-0.0001	-2.106*

(indicates ρ < 0.05, ** ρ < 0.01, *** ρ < 0.001)*

Table 24

Estimates for Regression Coefficient of Factors Affecting the Abundance of Waterbuck

Variable		estimate	std. error	95% confidence interval LL	UL	t-value
Habitat type (categorical)	Anogeissus	-0.240	0.128	-0.490	0.011	-1.873
	BTD	-0.267	0.126	-0.513	-0.021	-2.12***
Continuous	GG	0.00002	0.001	-0.003	0.003	0.016
	Water	-0.193	0.036	-0.264	-0.122	-5.31***
	Altitude	-0.002	0.0009	-0.004	-0.0001	-2.106*

(indicates ρ < 0.05 and *** ρ < 0.001)*

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Hartebeest distribution and abundance

Hartebeest also showed very low variability throughout the large number of events for the random effect, transect (variance = 0.481) indicating homogeneity has not been violated. There was also weak correlation between pairs of four continuous variables, grass greenness, grass biomass, distance to the boundary and elevation that predicted the distribution of hartebeest in the study area (Figure 52). There was no colinearity among these predictors, indicating independence in the continuous variables. There was a significant effect of the season, particularly dry season (-5.110 ± 0.573, C.I. = -6.234– - 3.986, $\rho < 0.001$, Table 25) and fire season (0.861 ± 0.236, C.I. = 0.399 – 1.323, $\rho < 0.001$, Table 25), on the distribution of the hartebeest. The rainy and flood seasons did not predict the distribution of hartebeest significantly, neither did the habitat types. Five continuous variables emerged to predict hartebeest distribution significantly; grass greenness (0.071 ± 0.002, C.I. = 0.004 – 0.013, $\rho < 0.001$, Table 25); grass biomass (0.958 ± 0.319, C.I. = 0.333–1.582; $\rho < 0.01$, Table 25); distance from the Park's boundary (0.040 ± 0.020, C.I. = 0.002 – 0.079, $\rho < 0.05$, Table 25); distance from nearest source of water (-0.164 ± 0.070, C.I. = -0.177 – -0.143, $\rho <$ 0.05, Table 25) and elevation (0.007 ± 0.002, C.I. = 0.003 – 0.01, $\rho < 0.001$, Table 25). For every 1% increase in percentage grass greenness, there was a very highly significant increase in the log odds of hartebeest presence by 0.009. For every 1 kg increase in grass biomass, there was a highly significant increase in the log odds of hartebeest presence by 0.958; for every 1 km distance away from the Park's boundary, there was a significant increase in the log odds of hartebeest

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presence by 0.040; for every 1 km distance away from nearest source of water, there was a significant decrease in the log odds of hartebeest presence by 0.164; and for every 1 m rise in altitude, there was a significant increase in the log odds of hartebeest presence by 0.007. The hartebeest were scarce in the dry season but

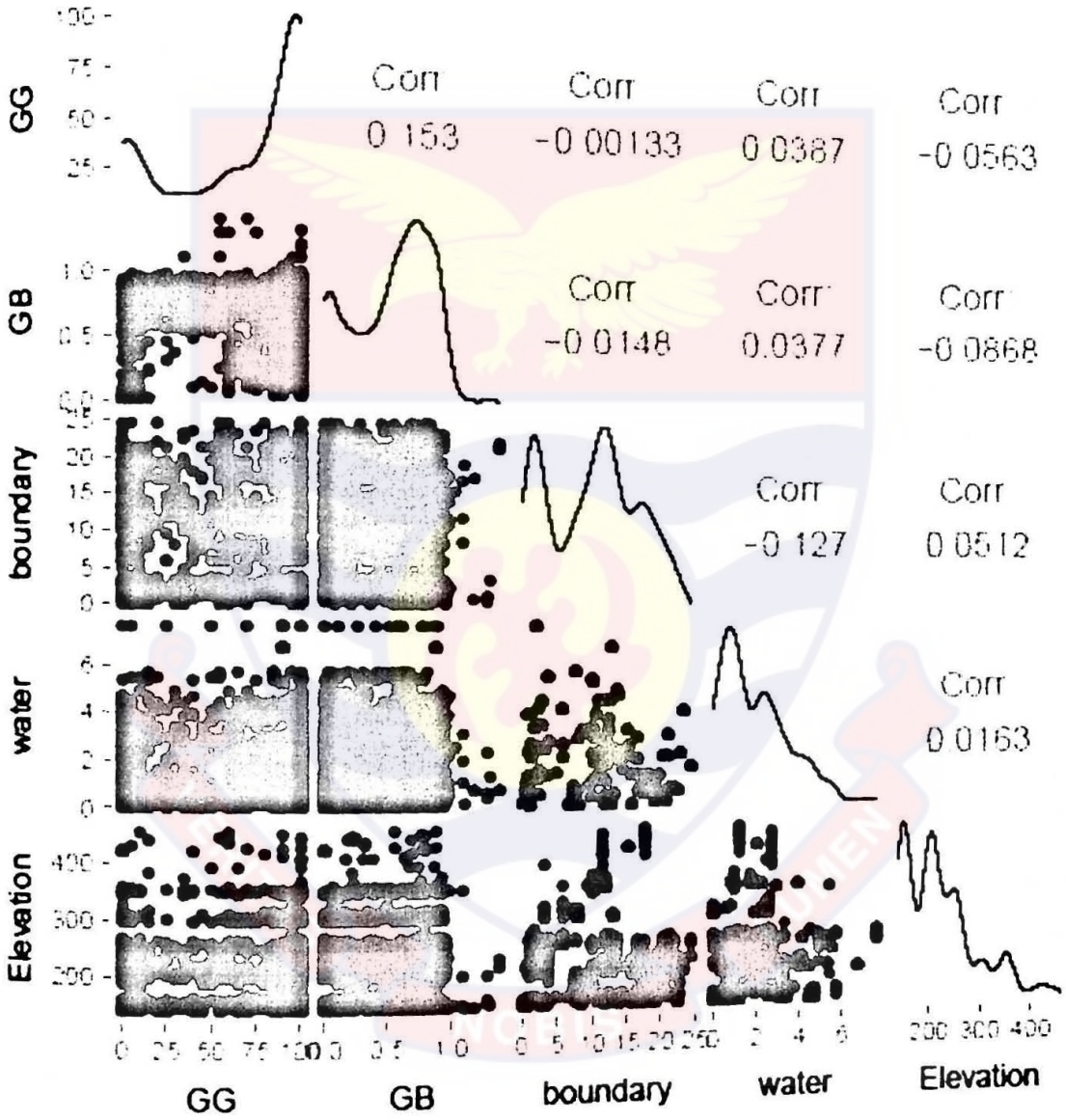


Figure 52: Panels showing distributions of continuous variables from the model predicting hartebeest spatial distribution, correlations between pairs of continuous variables and kernel densities (diagonal wiggles).

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Table 25

Estimates for Regression Coefficient of Factors Affecting the Distribution of Hartebeest

Variables		estimate	Std. Error	95% confidence interval		z-value	ρ
				LL	UL		
Season (categorical)	Dry	5.110	0.573	-6.234	-3.986	-8.912	0.000 ***
	Fire	0.861	0.236	0.399	1.323	3.654	0.000 ***
	Flood	-0.134	0.252	-0.627	0.359	-0.533	0.594
	Rainy	0.029	0.236	-0.434	0.493	0.124	0.902
Continuous	GG	0.009	0.002	0.004	0.013	3.612	0.000 ***
	GB	0.958	0.319	0.333	1.582	3.007	0.003**
	Boundary	0.040	0.020	0.002	0.079	2.052	0.040*
	Water	-0.164	0.071	-0.177	-0.143	-2.213	0.021*
	Elevation	0.007	0.002	0.003	0.010	3.979	0.000 ***

(indicates $\rho < 0.05$ **, $\rho < 0.01$ and *** $\rho < 0.001$*

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common in the fire season. They were found to be distributed in places at highlands far away the Park's boundaries where green grasses were obtainable in large quantities. Kingdon et al. (2013) reported hartebeest moving into more arid habitats after rains. However, in this study, rainy season did not predict the distribution of hartebeest significantly.

Seasonality did not significantly affect the hartebeest abundance and there was a significantly low hartebeest abundance in the BTD habitat type (- 0.338 ± 0.136, C.I. = -0.605 – -0.070, $\rho < 0.001$, Table 26). Other habitat types did not significantly influence the abundance of hartebeest in MNP. Percentage grass crude protein and distance from nearest source of water were also important variables that affected the hartebeest abundance. For every 1 % increase in percentage grass crude protein, there was a significant decrease in hartebeest abundance by 0.110 (-0.110 ± 0.056, C.I. = -0.219 – -0.001, $\rho < 0.05$, Table 26), indicating that hartebeest tended to be more abundant when grass has low crude protein. For every 1 km distance away from nearest source of water, there was a very highly significant decrease in hartebeest abundance by 0.225 (-0.225 ± 0.037, C.I. = -0.299 – -0.152, $\rho < 0.001$, Table 26), indicating that hartebeest tended to be more abundant near sources of water than farther away.

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Table 26

Estimates for Regression Coefficient of Factors Affecting the Abundance of Hartebeest

Variables		estimate	Std. error	95% confidence interval		t-value
				LL	UL	
Habitat type (Categorical)	Anogeissus	-0.228	0.178	-0.577	0.012	-1.284
	BTD	-0.338	0.136	-0.605	-0.070	-2.476 (*)
	BTV	-0.007	0.129	-0.261	0.245	-0.060
	Riverine	-0.078	0.245	-0.559	0.403	-0.319
	Swamp	-0.247	0.242	-0.722	0.228	-1.019
Continuous	GG	0.0004	0.001	-0.002	0.003	0.262
	GB	-0.397	0.206	-0.801	0.007	-1.927
	CP	-0.110	0.056	-0.219	-0.001	-1.978 (*)
	bdry	-0.007	0.012	-0.030	0.016	-0.595
	cty	0.009	0.012	-0.015	0.032	0.778
	water	-0.225	0.037	-0.299	-0.152	-6.04 (***)
	Elevation	-0.002	0.001	-0.004	0.001	-1.451

(indicates $\rho < 0.05$ and *** $\rho < 0.001$)*

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Kob distribution and abundance

Variability was low throughout the random effect, transect (variance = 0.846), which means that homogeneity was not violated. Figure 53 indicates there was independence of each continuous variable as correlations were very weak, and there were no strong linear relations between these predictors.

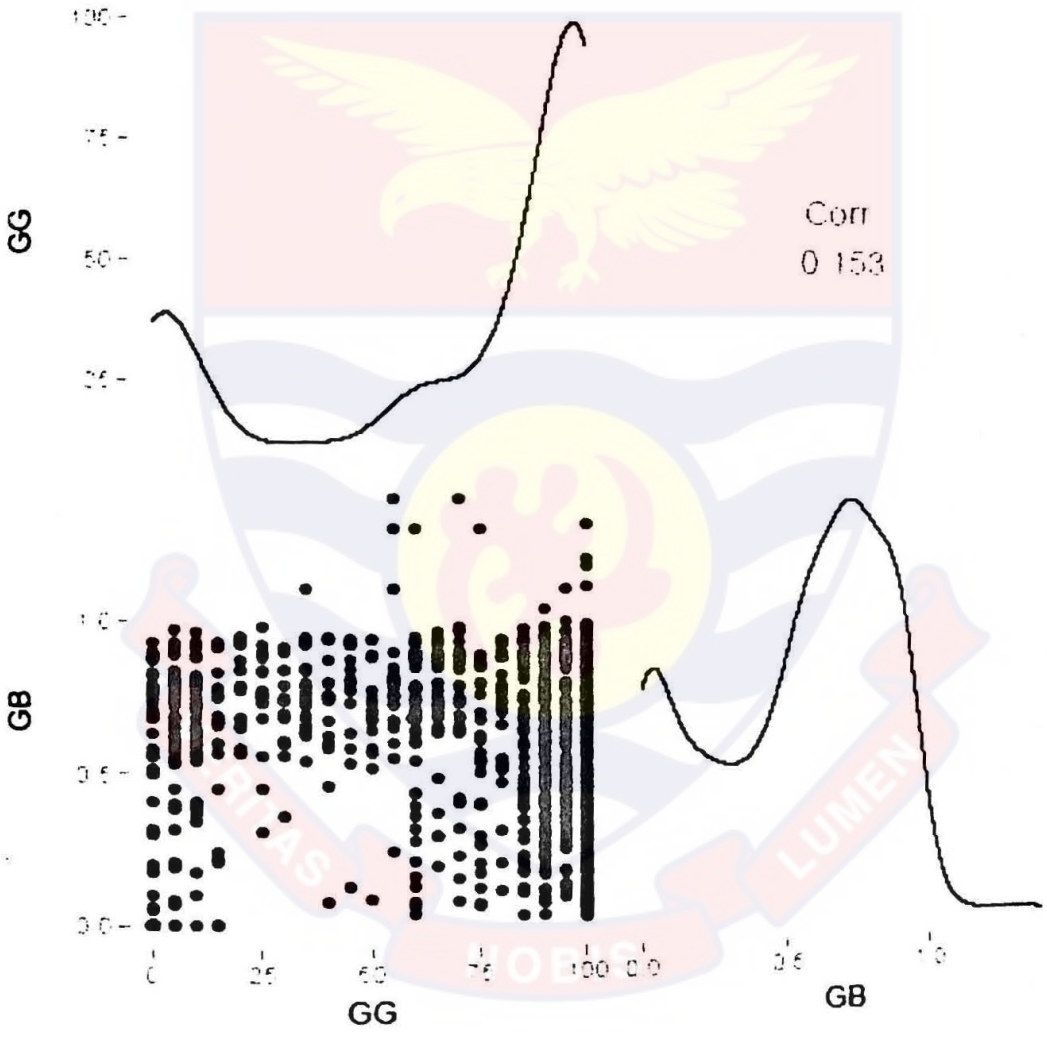


Figure 53: Panels showing distributions of continuous variables from the model predicting kob spatial distribution, correlations between continuous variables and kernel densities (diagonal wiggles).

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There was a significant prediction by the season on the distribution of the kob, particularly dry season (-2.210 ± 0.309, C.I. = -2.816– -1.603, $\rho < 0.001$, Table 27) and fire season (0.575 ± 0.186, C.I. = 0.209–0.940, $\rho < 0.01$, Table 27). The rainy and flood seasons did not predict the distribution of the kob significantly, or did the habitat types. Continuous variables, grass greenness (0.012 ± 0.002, C.I. = 0.008-0.016, $\rho < 0.001$, Table 27) and grass biomass (1.497 ± 0.259, C.I. = 0.988–2.006, $\rho < 0.001$, Table 27) predicted kob distribution in the Park significantly.

Table 27

Estimates for Regression Coefficient of Factors Affecting the Distribution of kob

Variables		estimate	std. error	95% confidence interval		z-value	ρ
				LL	UL		
Season	Dry	-2.210	0.309	-2.816	-1.603	-7.138	0.000***
(Categorical)	Fire	0.575	0.186	0.209	0.940	3.089	0.002 **
	Flood	-0.314	0.197	-0.670	0.075	-1.585	0.113
	Rainy	-0.043	0.182	-0.401	0.314	-0.238	0.812
Continuous	GG	0.012	0.002	0.008	0.016	5.896	0.000***
	GB	1.497	0.259	0.988	2.006	5.780	0.000***

*(** indicates $\rho < 0.01$, *** $\rho < 0.001$)*

For every 1% increase in percentage grass greenness, there was a significant increase in the log odds of kob presence by 0.012 and for every 1 kg/m^2 increase in grass biomass, there was a significant increase in the log odds of kob presence by 1.497. The kob were uncommon in the dry season but

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common in the fire season. They were distributed at places in the Park where green grasses were obtainable in large quantities. Variables such as flood, riverine habitats, elevation and distance to source of water did not predict their distribution significantly contrary to reports by Kingdon (1997) and Kingdon et al. (2013).

Seasonal variation affected kob abundance in MNP. There was significant abundance of kob in the dry season (1.306 ± 0.296, C.I. = 0.725–1.887, $\rho < 0.05$, Table 28) and in the fire season (-0.199 ± 0.076, C.I. = -0.348– -0.050, $\rho < 0.05$, Table 28). Effects of rainy and flood seasons on kob abundance were not significant. Also, kob abundance was significantly higher in the swamp (0.316 ± 0.118, C.I. = 0.084–0.548, $\rho < 0.05$, Table 28). Other habitat types did not significantly influence the abundance of kob in MNP. Percentage grass greenness, grass biomass, distance from the nearest source of water and altitude were the continuous variables that significantly affected kob abundance. For every 1% increase in percentage grass greenness, there was a very highly significant decrease in kob abundance by 0.004 (-0.004 ± 0.001, C.I. = -0.006– -0.002, $\rho < 0.001$, Table 28) indicating that kob tended to be less abundant when percentage grass greenness was high. For every 1 kg/m^2 increase in grass biomass, there was a highly significant decrease in kob abundance by 0.364 (-0.364 ± 0.129, C.I. = -0.616– -0.111, $\rho < 0.01$, Table 28) indicating that kob tended to be less abundant when grass biomass was high. For every 1 km distance away from nearest source of water, there was a very highly significant decrease in kob abundance by 0.153 (-0.153 ± 0.023, C.I. = -0.198– -0.107, $\rho < 0.001$, Table 28). Also, for every 1 m rise in altitude above sea level, there was a very highly significant decrease in kob

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abundance by 0.003 (-0.003 ± 0.001, C.I. = -0.005– -0.002, $\rho < 0.01$, Table 28). Kob tended to be more abundant near sources of water than farther away and in low altitudes than high altitudes.

Table 28

Estimates for Regression Coefficient of Factors Affecting the Abundance of kob

Variables		estimate	std. error	95% confidence interval LL	UL	t-value
Season (categorical)	Dry	1.306	0.296	0.725	1.887	4.405*
	Fire	-0.199	0.076	-0.348	-0.050	-2.612*
Habitat type (categorical)	Swamp	0.316	0.118	0.084	0.548	2.668*
Continuous	GG	-0.004	0.001	-0.006	-0.002	-3.76***
	GB	-0.364	0.129	-0.616	-0.111	-2.82**
	Water	-0.153	0.023	-0.198	-0.107	-6.60***
	Altitude	-0.003	0.001	-0.005	-0.002	-4.63***

(Indicates $\rho < 0.05$, ** indicates $\rho < 0.01$ and *** $\rho < 0.001$)*

Warthog distribution and abundance

Variability was low in the random effect, transect (variance = 0.234). The fire season seemed to have introduced a slight increase in variability (Figure 54) but this did not violate homogeneity as there was still substantial overlap.

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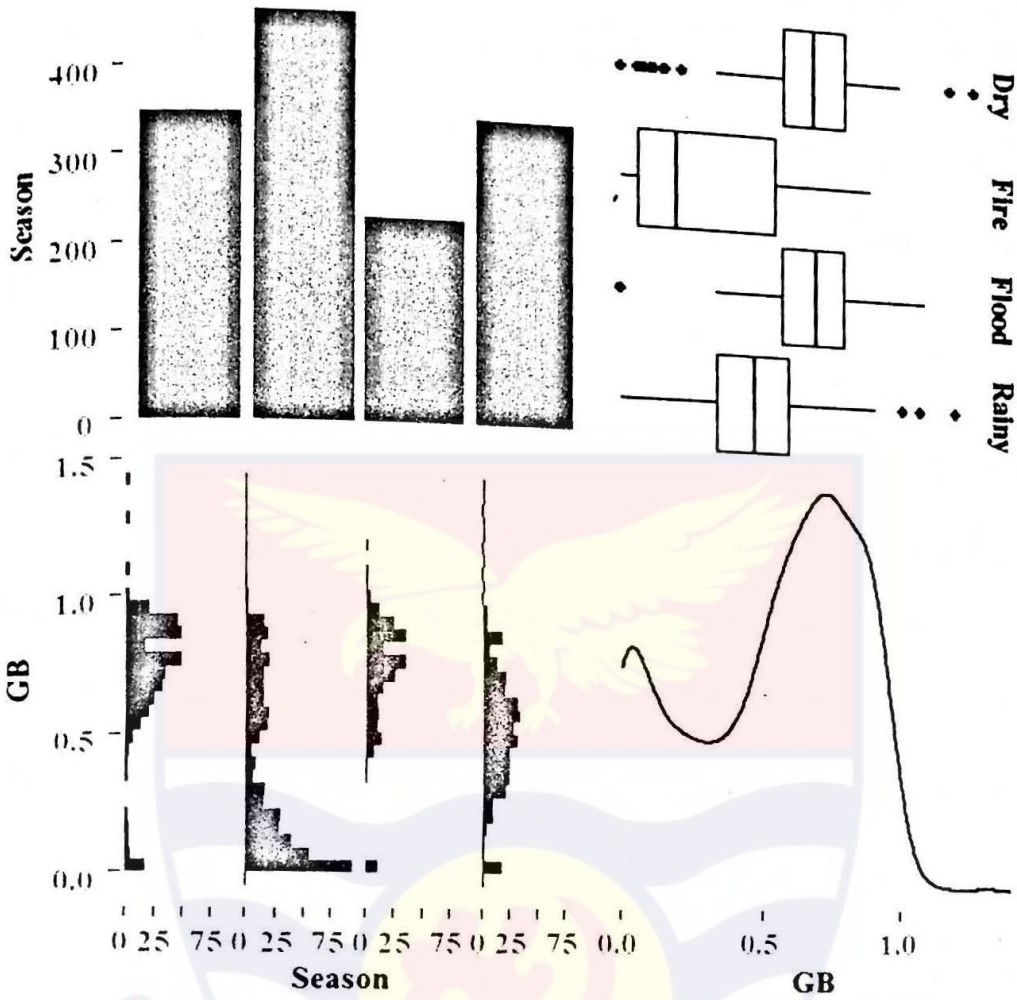


Figure 54: Seasonal effect on the distribution of grass biomass for warthog.and the kernel density (wiggle in bottom-right) of grass biomass.

The fire season was more prolonged but had relatively very low grass biomass, and did not affect the distribution of warthog significantly. Only the dry season (-1.569 ± 0.314, C.I. = -2.185– -0.953, $\rho < 0.001$, Table 29) and the flood season (0.565 ± 0.194, C.I. = -0.945– -0.186, $\rho < 0.01$, Table 29) affected the distribution of warthog significantly. While the warthog tended to be uncommon during the dry season, they became common during the flood season. Grass biomass was the only continuous variable that predicted the distribution of

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warthog significantly (1.177 ± 0.244, C.I. = 0.699–1.656, $\rho < 0.001$, Table 29). For every 1 kg/m^2 increase in grass biomass, there was a very highly significant increase in the log odds of warthog presence by 1.177. Thus, warthog tended to inhabit areas where there was increased grass quantity (grass biomass or grass cover).

There was no significant seasonal variation in the abundance of warthog in MNP. Warthog abundance was significantly low in the BTD (-0.263 ± 0.099, C.I. = -0.458– -067, $\rho < 0.05$, Table 30) but significantly high in the swamp (0.300 ± 0.134, C.I. = 0.036–0.565, $\rho < 0.05$, Table 30). Other habitat types did not significantly influence the abundance of warthog in MNP. Percentage grass greenness, distance from nearest source of water and altitude were the continuous variables that significantly affected warthog abundance. For every 1% increase in percentage grass greenness, there was a very highly significant decrease in warthog abundance by 0.002 (-0.002 ± 0.001, C.I. = -0.004– -0.00004, $\rho < 0.05$, Table 30) indicating that warthog tended to be less abundant when percentage grass greenness was high. For every 1 km distance away from nearest source of water, there was a very highly significant decrease in warthog abundance by -0.170 (-0.170 ± 0.026, C.I. = -0.221– -0.119, $\rho < 0.001$, Table 30) indicating that warthog tended to be more abundant near sources of water than farther away. Also, for every 1 m rise in altitude above sea level, there was a very highly significant decrease in warthog abundance by 0.002 (-0.002 ± 0.0008, C.I. = -0.004– -0.007, $\rho < 0.01$, Table 30) indicating that warthog were more abundant in low altitudes than high altitudes.

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Table 29

Estimates for Regression Coefficient of Factors Affecting Warthog Distribution

Variables		estimate	std. error	95% confidence interval		z-value	ρ
				LL	UL		
Season (categorical)	Dry	-1.569	0.314	-2.185	-0.953	-4.992	0.000***
	Fire	0.329	0.180	-0.023	0.681	1.830	0.067
	Flood	0.565	0.194	-0.945	-0.186	-2.917	0.004 **
	Rainy	0.118	0.172	-0.219	0.455	0.686	0.493
Continuous	GB	1.177	0.244	0.699	1.656	4.826	0.000***

*(** indicates ρ < 0.01 and *** ρ < 0.001)*

Table 30

Estimates for Regression Coefficient of Factors Affecting Warthog Abundance

Variables		estimate	std. error	95% confidence interval		t-value
				LL	UL	
Habitat type (categorical)	BTD	-0.263	0.099	-0.458	-0.067	-2.634*
	Swamp	0.300	0.134	0.036	0.565	2.235*
Continuous	GG	-0.002	0.001	-0.004	-0.0004	-1.994*
	Water	-0.170	0.026	-0.221	-0.119	-6.53 ***
	Altitude	-0.002	0.0008	-0.004	-0.0007	-2.861 **

(indicates ρ < 0.05, ** ρ < 0.01 and *** ρ < 0.01)*

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Bushbuck distribution and abundance

There was a not significant correlation between the two continuous variables, grass greenness and grass biomass in the final model (Figure 55), meaning that they were independent. Variability in the random effect, transect, was low (variance = 0.6071) and so the assumption of homogeneity was not violated. There was a seasonal effect on the distribution of bushbuck. Dry season (-1.820 ± 0.292, C.I. = -2.393– -1.247, $\rho < 0.001$, Table 31) and flood season (-0.737 ± 0.201, C.I. = -1.131– -0.344, $\rho < 0.001$, Table 31) significantly affected the distribution of bushbuck but the rainy and fire seasons did not. Bushbuck were scarce in both the dry and flood seasons. Habitat types also did not predict the distribution of bushbuck significantly. Two variables emerged to predict the distribution of bushbuck significantly: grass greenness (0.009 ± 0.002, C.I. = 0.006–0.013, $\rho < 0.001$, Table 31) and grass biomass (1.131 ± 0.255, C.I. = 0.630-1.632, $\rho < 0.001$, Table 31). For every 1% increase in grass greenness, there was a significant increase in bushbuck presence by 0.009 and for every 1 kg/m^2 grass biomass, there was a significant increase in the log odds of bushbuck presence by 1.131. Bushbuck inhabited places where green (fresh) grasses were obtainable in large quantities.

There was a significant effect of dry season on the abundance of bushbuck in MNP (1.114 ± 0.287, C.I. = 0.551 – 1.677, $\rho < 0.05$, Table 32) as bushbuck tended to be more abundant in the dry season. There was no significant effect of other seasons on the abundance of bushbuck and also habitat types did not significantly influence the abundance of bushbuck in MNP. Distance from nearest

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source of water and altitude were the only two continuous variables that significantly affected bushbuck abundance. For every 1 km distance away from nearest source of water, there was a very highly significant decrease in bushbuck abundance by 0.140 (-0.140 ± 0.022, C.I. = - 0.183– -0.096, $\rho < 0.001$, Table 32) indicating that bushbuck tended to be more abundant near sources of water than farther away. For every 1 m rise in altitude above sea level, there was a very highly significant decrease in bushbuck abundance by 0.004 (-0.004 ± 0.001, C.I. = -0.005– -0.002, $\rho < 0.001$, Table 32) indicating that bushbuck tended to be more abundant in low altitudes than high altitudes.

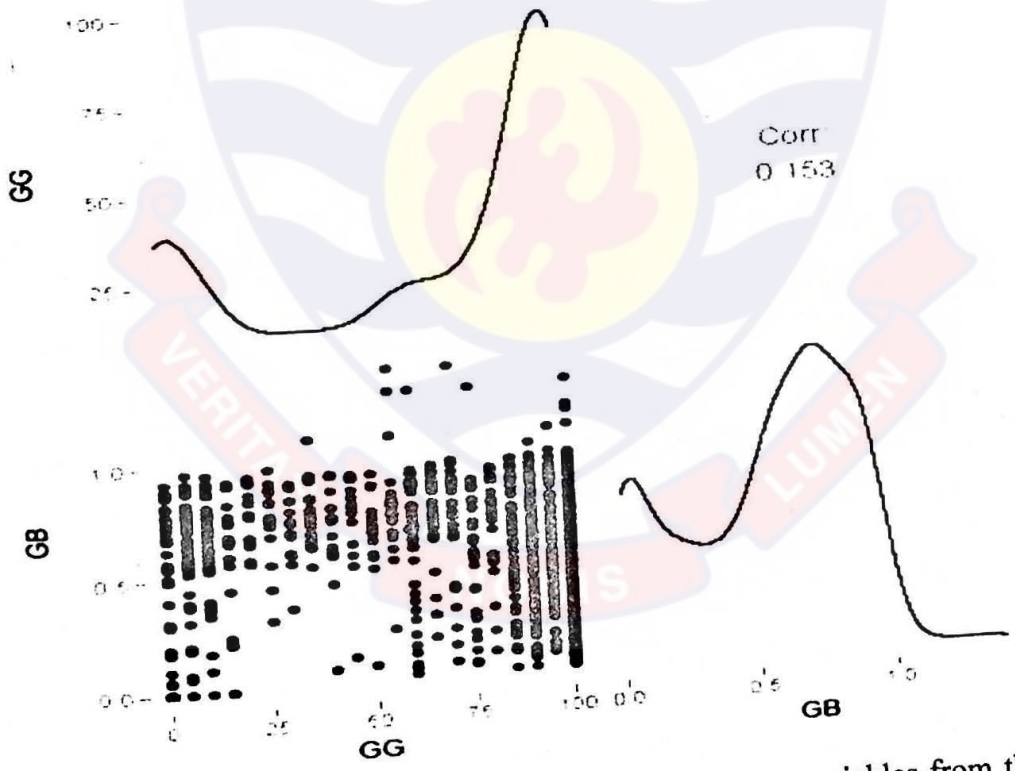


Figure 55: Panels showing distributions of continuous variables from the model predicting bushbuck spatial distribution, correlations between continuous variables and kernel densities (diagonal wiggles).

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Table 31

Estimates for Regression Coefficientof Factors Affecting Bushbuck Distribution

Variables		estimate	std. error	95% confidence interval		z-value	ρ
				LL	UL		
Season	Dry	-1.820	0.292	-2.393	-1.247	-6.227	0.000***
(categorical)	Fire	0.267	0.184	-0.093	0.627	1.454	0.146
	Flood	-0.737	0.201	-1.131	-0.344	-3.670	0.000***
	Rainy	-0.168	0.180	-0.521	0.185	-0.931	0.352
Continuous	GG	0.009	0.002	0.006	0.013	4.845	0.000***
	GB	1.131	0.255	0.630	1.632	4.427	0.000***

*(*** indicates ρ < 0.001).*

Table 32

Estimates for Regression Coefficient of Factors Affecting Bushbuck Abundance

Variables		estimate	std. error	95% confidence interval		t-value
				LL	UL	
Season (categorical)	Dry	1.114	0.287	0.551	1.677	3.878*
	Fire	-0.116	0.080	-0.274	0.042	-1.442
	Flood	0.015	0.087	-0.156	0.185	0.166
	Rainy	0.089	0.075	-0.058	0.2364	1.183
Continuous	Water	-0.140	0.022	-0.183	-0.096	-6.29***
	Altitude	-0.004	0.001	-0.005	-0.002	-4.60***

(* indicates ρ < 0.05 and *** ρ < 0.001)

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Summary of distribution and abundance of grazers.

Grass biomass was the most important predictor of large grazer distribution in the Park and this underlines the importance of grass quantity to the large grazers. Only three large grazers were not predicted significantly by grass biomass or grass cover (Table 33). Green grass was another important variable, predicting 50% of the large grazers. While grass quality was expected to be an important predictor of large grazer distribution, the low number of observations with respect to DOM and CP probably affected the results. Percentage crude protein did not significantly predict the distribution of any of the eight large grazers and percentage digestible organic matter predicted only roan antelope distribution significantly (Table 33). Anthropogenic factors were the next important predictors. More hartebeest and buffalo tended to be distributed farther away from the Park's boundary and more roan antelope tended to be distributed farther away from the communities. The topography of the Park was also important as more hartebeest tended to occur at higher altitudes than lower altitudes but more waterbuck tended to occur at lower altitudes than higher altitudes. Two variables, distance from the nearest source of water and altitude emerged as most important for the abundance of the large grazers studied. All the grazers were abundant near sources of water and all were more abundant at lower altitudes than higher except the warthog, which was more abundant at higher altitudes, and buffalo and hartebeest that were not significantly influenced by altitude (Table 33).

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Table 33

Large Grazers and Variables that Predict their Distribution and Affect their Abundance Significantly

Variables	Elephant	Buffalo	Roan	Waterbuck	Hartebeest	Kob	Warthog	Bushbuck
GG			√		√	√*	*	√
GB/ĠC				√	√	√*	√	√
CP					*			
DOM			√					
Boundary		√			√			
Community			√					
Water	*	*	*	*	√*	*	*	*
Elevation	*		*	√*	√	*	*	*
Dry season	√		√		√	√*	√	√*

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Table 33, continued

Variables	Elephant	Buffalo	Roan	Waterbuck	Hartebeest	Kob	Warthog	Bushbuck
Fire season			√		√	√*		
Rainy season								
Flood season							√	√
Anogeissus	*	√		*				
BTD		√		√	*		*	
BTV		√		√				
Riverine		√		√				
Swamp		√				*	*	

*(√ = significant Prediction of Distribution; * = Significant Effect on Abundance)*

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CHAPTER FIVE: DISCUSSION

Climate and Land Cover Changes

Despite its associated errors, remote sensing remains the best option for acquiring quantitative data on land cover for change detection studies. The use of Landsat satellite imagery in change detection is limited by the effect of weather and other "noise" producing obstacles that interfere with the output of these passive sensors. Also, the spectrometers measure signals at several spectral bands simultaneously, resulting in multispectral images with multiple interpretations (Lamprey, 1984). Despite these limitations, Landsat satellite ecological application is still widely used by researchers to monitor land cover and land use changes. Few researchers have published results on change detection studies with high resolution remote sensing data in Africa's PAs (Mwalyosi, 1992; Lamprey). Considering that the overall ground truth validation accuracy was 80.3%, the 19.7% error in this study implied that the Landsat satellite output was not perfect, but this was to be expected. However, the accuracy was high enough for the interpretation of the imagery.

The results indicated a rise in temperature that became significant after two decades and a reduction in the amount of rainfall every decade. There seemed to be an inverse relationship between temperature and rainfall in the MNP so that when there is a high mean temperature, there is a correspondingly low mean rainfall and *vice versa*. The effect of rainfall on the MNP ecosystem cannot be over-emphasized. For example, the ability of trees and grasses to make good use of soil moisture, is primarily determined by rainfall (Scholes & Archer, 1997).

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While the effect of rainfall on grass at MNP was immediate, there was a time lag in the case of trees. Thus, in terms of forage, there was a correspondingly immediate benefit of rainfall to the large grazers. As rainfall affected primary productivity (e.g. East, 1984; Bonnet et al., 2010), so did forage quality and quantity vary seasonally as noted previously by Fryxell & Sinclair (1988). Whilst forage quantity was inversely related to quality (Fryxell, 1991), both reached a peak during the flood season, with a sharp decline to the trough in the fire season. Seasonal rainfall can refill ephemeral water sources, triggering the assemblage of large numbers of animals in such areas that were otherwise unselected during the dry season (Western, 1975). Temperature follows a similar pattern inversely, though with narrow variations, so that seasonal effects of temperature may result in drying of most water sources that compel large numbers of animals to concentrate around few water holes in MNP. Forecastsfor the next seven years suggest a continuum of slight increases in mean rainfall following a four-year sharp drop in annual mean rainfall at MNP. This is an indication that between 2010 and 2020 shrub-land and grassland are likely to shrink and open and closed savanna woodland expand. Accordingly, there will be shrinking forage resources for the grazers and abundant forage for the browsers during the period.

Density and Population Trends

Many researchers (Eltringham, 1979; Sinclair, 1985; Mooring & Mundy, 1996) used road transects to collect count data despite their many flaws, including the high possibility of failing to follow random routes across diverse habitat types, which are, therefore, either over or under sampled. In this study, road transects

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used represented ample habitat heterogeneity that minimizes bias. However, the open plain habitats, Anogeissus, BTD and BTV could be over-sampled since they were easier to traverse.

Detectability may also influence the outcome of the analysis. Because the mammals have different sizes, they have different chances of being detected. One option was to assign each species a visibility factor per habitat type but this could complicate the data collection with as many as eight species involved. However, the decision to study grazers as large as at least 60 kg in mean body mass and the total search effort minimized bias. Nonetheless, it is very likely that buffalo were underestimated because they are nocturnal, grazing for an average 3-4 hours of daytime activity (Kingdon, 1997) and therefore there is a higher chance of missing them.

It is envisaged that if future studies will improve in terms of the size of MNP sampled, the accuracy of the population estimates of large grazers will also improve. However, the increasing population trend is a sign of improved management efforts towards species protection and conservation. Considering the value of the estimated densities of the large grazers studied in relation to the size of MNP with its habitat heterogeneity and forage abundance, there is no doubt the potential for further increases in populations of these mammals. The study also supported the hypothesis of variation in population trends of different species attributed to different responses to environmental changes.

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Habitat Selectivity

One of the disadvantages of the selection index of Jacobs (1974) is inability to test the statistical significance. However, it was successful in differentiating habitat selection and avoidance pattern by all the large grazers studied. While some of the large grazers in the MNP showed distinct seasonal patterns of habitat selection and use, others like roan antelope and hartebeest showed unclear patterns. This underscores the possibility of the effect of multiple factors than forage alone on habitat selection by the large grazers.

The results of this study confirmed observations by other researchers (Western, 1975; Sinclair, 1985; Ben-Shahar & Skinner, 1988; Gordon, 1989; McNaughton, 1990; Ben-Shahar & Coe, 1992; Owen-Smith, 1992; Fritz et al., 1996; Omphile, 1997; Mwangi & Western, 1998; Bergstrom & Skarpe, 1999) on inter-habitat shifts by grazers in response to distinct resource diversities. However, the fine-scale mosaics of habitats that characterize the MNP complicates patterns of seasonal habitat selection. This could influence the results of this study and obscure the patterns of habitat selection and use for some grazers since grazers could be sighted in areas that they did not intend to select while they were in transit to forage in other areas.

Generally, the large grazers at MNP were less selective especially during the rainy and flood seasons and more especially during the fire season. However, because there was shrinkage of habitat resources caused by fire, selectivity was obviously low in the fire season. Previous studies (Gordon, 1989; Fritz et al., 1996), confirmed the hypothesis that there is low selectivity when forage

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abundance is high and high selectivity when forage abundance is low. However, in this study factors other than forage abundance may account for selectivity. For example, forage diversity (such as the distribution of different plant communities), plant productivity and variations in availability in different habitats can affect habitat selection by large grazers of MNP in different ways. Also, it is envisaged that for the relatively small body-sized large grazers, predation is an important factor to consider in habitat selection. Kob, warthog and bushbuck appeared to have avoided the open plains-Anogeissus, and especially, BTD and BTV, and this may be a response to predation in MNP. Nevertheless, it seems that the swamp and riverine habitats presented abundant forage to kob, warthog and bushbuck in accordance with the hypothesis. The waterbuck were highly selective in all seasons in their preferred swamps. This is because of their nature as wetland antelopes (Kingdon, 1997), but this also means low forage abundance for them. Apart from the Boval, the habitat least preferred by roan antelope is the swamp to which they shift in the dry season. The fact that the fire season depicts all the dry season conditions in the swamp but roan antelope still avoided the swamp in the fire season explains why fire is a resource limiting factor-clearing forage during this season. Still, other factors must enable elephant, waterbuck, hartebeest, kob, warthog and bushbuck select and use the swamp in the fire season. For example, elephant are browsers as well and they can switch between grazing and browsing. Second, ecological barriers (e.g. altitude) may restrict the movement of some of these grazers. Waterbuck, for instance, are known to be lowland species while most swamps are formed at lowlands. The hartebeest, like roan antelope probably

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avoided pools of water and muddy substratum and therefore used the swamp during the fire season but the hartebeest probably did not encounter fire incidence in all the sampling events. Third, the fine scale mosaic of habitats probably interfered with, and complicated the patterns of habitat selection and use.

The shift of the buffalo to the swamp during the rainy season is difficult to explain because naturally, buffalo prefer drier grounds (Kingdon, 1997). It is possible that the shift was necessary to allow open plains of Anogeissus to recover from the heavy grazing endured during the dry and fire seasons. The shift to swamp in the dry season by elephant was necessary due to their water requirements. While elephant will drink every day, they can only meet their water requirement during the dry season by locating the water holes created near the swamp in the MNP.

It was not possible in this study to ascertain the abundance status of food resources quantitatively, and so whether food resources were limiting or not remained unknown. Therefore, there was no basis to declare competition with confidence. However, in this study, results from habitat-use overlap indices were not consistent with conditions for interspecific competition among grazers for food (de Boer and Prins, 1990), which therefore could not account for habitat selection or use patterns and association between the grazer species.

Forage Quality and Quantity and Resource Use Overlap

Habitat overlap indices reflect the degree to which animals use the same habitat. These indices are very important because they are measures for

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competition interaction events in an ecosystem such as the MNP. When habitat overlap indices are high, competition is occurring and when the indices are low, competition is not occurring (Jenkins & Wright, 1988; Putman, 1996). However, high habitat overlap indices could also indicate an absence of competition permitting a sharing of common resources (Gordon & Illius, 1989; Putman). In this study, the degree of habitat overlap varied between large grazer species, between habitat types and between seasons. Abrams (1980) is of the view that the criteria for competition interactions is not fulfilled by resource use overlap exclusively, but also the strength of competition is determined by the density of individuals per the resource base in space and time.

Kob density was the highest and seemed to have overlap interactions more than any other large grazer while buffalo densities was the lowest and overlapped with others the poorest. Waterbuck also with a relatively low density overlapped very poorly with others. Competition, if occurring at all between kob and the other large grazers, may be only minor but that kob were more adapted to the MNP habitats and general environment than others. The poor overlap of waterbuck with others is more likely to be due to habitat preference while the gregarious life style of buffalo in addition to being a megagrazer may impose proximity restrictions to most of the other species. Resource use overlaps between the natural guild of large grazers in MNP (elephant, buffalo, roan antelope, waterbuck, hartebeest, kob, warthog and bushbuck) were generally low, which may also imply that interspecific competition played only a minor role in population dynamics even at high density.

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Low overlap in the various habitat types in MNP during the dry and rainy seasons may imply that there was high forage quality and quantity. Indeed, green grasses were available throughout the rainy and flood seasons and abundant throughout the flood season and most of the rainy season; and grass quantity was also very high throughout the dry and flood seasons, and part of the rainy season. It means that the large grazers responded to forage swelling in the rainy, flood and dry seasons by avoiding resource use overlaps, which allowed no competition to occur. However, the comparatively very high overlaps between pairs of the large grazers in the fire season may be due to resource constraints caused by grass clearance and this more likely allowed some degree of competition. The total surface of burnt area was very large, and therefore there was a significant shrinkage and the large grazers responded to forage shrinkage in the fire season by a high degree of resource overlaps and competition among themselves. These observations are consistent with the hypothesis that there are high resource use overlaps among co-existing grazers when forage is low in quality and quantity and low overlaps when forage is high in quality and quantity (Putman).

It appears that the fire season is considered to be a determinant of the number of individuals an area can hold under resource stressed conditions, whereas dry, rainy and flood seasons determine condition of the animals as food is abundant with low and high qualities for dry season, on the one hand, and rainy and flood seasons on the other, respectively. It is not justified yet whether fire season's forage were in limited supply on grazers densities with the present stocking rates of grazers studied, but this is a fair assumption considering the vast

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area of forage that were lost or inaccessible due to fire. Therefore, as far as grazing resources are concerned, MNP switched seasonally from resource abundance when competition did not occur to resource stressed conditions which allowed some degree of competition.

There are clear seasonal and habitat variations in inter-specific resource use overlap between the large grazers at MNP but whether these correspond with temporal and large-scale (geographical) spatial variations in inter-specific resource use overlap is uncertain. However, because the study took place over just one year, and was also restricted to the small confinement of MNP, these will remain uncertain, but there may be both temporal and spatial variation in the potential for competition for a given pair of species as suggested by Belovsky (1984, 1986). Therefore resource use overlap, or if it leads to competition, would still occur outside the boundaries of MNP, meaning that expansion of the reserve would not be a necessary management agenda in the conservation of the large grazers in this respect. Other sources of variation in resource use overlap, such as sex dependence (Gordon & Illius, 1989) and the opportunity for resource partitioning, were not evaluated. Further, there are several other important mechanisms of interaction among grazers apart from competition that were not evaluated. For example, grazing may increase primary production and quality of forage and thus lead to facilitation (McNaughton 1976; Gordon & Illius, 1988; Alpe, Kingery, & Mosley, 1999), and may also remove cover that is important for hiding and thus lead to higher levels of predation (Loft, Menke, Kie, & Bertram, 1987).

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Hutchinson's co-existence rule

The low habitat heterogeneity of MNP rather than its relatively small size plays a part in its low species-packing or high body weight ratio (WR). As the body WR of grazers of the MNP (1.40) was less than the theoretical expected ratio of approximately 2.0 (Hutchinson, 1959), it is suggested that in theory, the grazers at MNP were too closely packed or were too similar in body weight to co-exist according to the Hutchinson's Rule. Therefore, the results did not support the Hutchinson's Rule as there were several species with similar body weight co-existing within the grazer assemblage of the MNP. Similar conclusions can be drawn for other conservation areas in southern Africa to confirm the conclusions of Bonyongo and Harris (2007) because none of them had a degree of species-packing closer to the theoretically expected value of approximately 2.0.

Similar body weight co-existence was not much observed for larger grazers weighing more than 80 kg, but it was common to grazers less than 80 kg that accounted for about 71% of the species richness which was most likely the reason for the low species-packing at MNP. These included grazers in weight range from 3.6-5.2 kg. Examples include rock hyrax (*Procavia capensis*), colobus monkey (*Colobus vellerosus*), cane rat (*Thryonomys swinderianus*) and green monkey (*Cercopithecus aethiops*). Grazers in the weight range 12-14.1 kg include grey duiker (*Sylvicapra grimmia*), red-flanked duiker (*Cephalophus rufilatus*) and oribi (*Ourebia ourebi*) while grazers in the weight range 59-60 kg include yellow-

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back duiker (*Cephalophus silvicultor*) and bushbuck (*Tragelaphus scriptus*), and from 73.5–78.5 kg are warthog (*Phacochoerus aethiopicus*) and kob (*Kobus kob*).

Owen-Smith (1992) and Tokeshi (1999) proposed that species of similar weight evolve distinct morphological and behavioural patterns for habitat selection, which allow them clear ecological separation by their different resource use habits. For example, warthog (73.5 kg) and kob (78.5 kg) co-exist despite similarities in body weight because warthog is a mixed feeder, feeding on grass and other food material while kob is a full time grazer which makes them ecologically separated, hence their ability to co-exist at MNP. Ecological separation is well studied (Bell, 1982; Biggs, 1979; Burns & Griffin, 2000; Kingdon, 1997; Voeten & Prins, 1999). According to Kingdon, roan antelope select localities with minimal competition irrespective of the herbaceous species composition. In the Okavango Delta (Botswana), roan and sable antelope occur in low densities in the panhandle area where zebra and wildebeest densities are low (Burns & Griffin). Waterbuck also occur in low densities, preferring dense riverine woodlands near permanent waters, a habitat type largely avoided by zebra, wildebeest, roan and sable (Biggs, Kingdon). Lechwe (*Kobus leche*) (91 kg), tsetsebe (*Damaliscus lulatus*) (119 kg), ostrich (*Struthio camelus*) (120 kg) are among the sets of co-existing grazers with similar body weight. Although both lechwe and tsetsebe use floodplain vegetation (Biggs; Kingdon), they are ecologically separated as lechwe select wetter areas of the floodplains while tsetsebe graze along the margins. At MNP wet areas are not common all year

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round. Flood plains had dried up with only a few water holes created near the motel being available in the dry and fire seasons.

Species may also compete for a common resource, without being limited because they utilize the resource differently (resource partitioning), which allows co-existence. Though resource partitioning was not the focus of this study it is a possible phenomenon that allows grazers at MNP to co-exist. For instance, Bonyongo and Harris (2007) showed that zebra feeding habitats in the Okavango Delta include sites with a high standing crop while wildebeest and tsetsebe generally selected sites characterized by shorter swards with high leaf to stem ratio allowing them to co-exist.

Holes in grazer assemblages

Generally, MNP, Okavango Delta, Etosha, Hwange and Kafue are deficient in species within the 10–30 kg body weight range, whereas Kruger has a high number of species in this range (Bonyongo, & Harris, 2007). Most species within the range like klipspringer (*Oreotragus oreotragus*), grey rhebok (*Kobus vardoni*), vaal rhebok (*Pelea capreolus*) and mountain reedbuck (*Redunca fulvorufula*) prefer habitats characterized by hills and rock outcrops with short grasses (Kingdon, 1997), a habitat type common in Kruger. MNP is further deficient in species within the 80–260 kg body weight range. However, the grazers in this body weight range are usually temperate mammals. Potentially, the Bohor reedbuck (*Redunca redunca*) may also be expected to occur in MNP. The current Management Plan indicates few encounters with the Bohor reedbuck in MNP (WD, 2011), but this remains unconfirmed officially, which may lend

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credence to a possible existence of a very low remnant population of the Bohor reedbuck that may have resulted from the historical massacre of mammals in MNP (WD). Such a population bottleneck could result in a permanently low population or extinction. The massacre may also have caused extirpation of the giraffe from MNP, a speculation that has never been confirmed, even though accounts from early management staff (*pers comm*) suggested that the species used to occur in MNP. It is likely that the giraffe (*Giraffa camelopardis*) faced local extinction before 1957 when the massacre of mammals ceased, or a small remnant population could not survive the loss of fitness.

Beyond 1,000 kg, there were apparently too few grazers in all the six areas investigated, and in the African assemblage as a whole, as noted by Bonyongo & Harris (2007). The apparent lack of mega-grazers has been linked to Pleistocene extinctions. Mega-grazers which became extinct during the Pleistocene were the giant hippo (*Hippopotamus gorgops*), the giant hartebeest (*Megalotragus priscus*) (extinct 12,000 years ago) and the giant buffalo (*Pelorovis antiquus*) that became extinct 4000 years ago (Owen-Smith, 1992; Prins & Olff, 1998, Bonyongo & Harris). It is therefore likely that the African elephant (*Loxodonta africana*) lacked potential competitors.

Conservation action

There is a high possibility that the Bohor reedbuck lives at MNP, therefore more active measures to identify, protect and manage its populations is necessary. According to IUCN (2008), the Bohor reedbuck are associated with woodland and floodplain grassland across much of their range. They are effectively water-

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dependent grazers, but show a strong preference for extensive areas of flood plains and open inundated grasslands where access to water may become restricted in the dry season. The MNP offers all these habitat conditions favourably to the Bohor reedbuck except water availability in the floodplains during the dry season, which must be one of the management priorities for its conservation. The giraffe will fit in a gap within the body size rank order and so can co-exist with adjacent grazers at MNP and with suitable habitats there is no doubt that the conservation of giraffe will be successful if it is re-introduced.

Body Size Differentiation

Owen-Smith (1988) reported that herbivores show an interspecific decrease in food quality with increasing body mass. Indeed, it is widely accepted that herbivore body size determines energy demands (Bell, 1969; Bell, 1970; Bell, 1971; McNaughton & Georgiadis, 1986). Allometry involves the relationship between an organism's body size and biological function and it has been proposed that allometric feeding strategies account for high forage selectivity among small grazers (Du Toit & Cumming, 1999) and low selectivity or indiscriminate feeding among larger grazers (Demment & Van Soest, 1985; McNaughton & Georgiadis; Illius, 1997). For large-bodied grazers, large amounts of forage with high amounts of quality fibre are important for their energetic demands (Owen-Smith). However, because high quality forage is rare in large amounts (Owen-Smith), and large grazers have to feed selectively, this is not possible because they have to ingest large amounts of food per day and also their larger muzzles restrict their selectivity (Owen-Smith). Accordingly large-bodied grazers feed indiscriminately

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for large quantities of forage on resources with relatively low nutritional value (Owen-Smith & Novellie, 1982; Belovsky, 1984) that are widely distributed across the landscape (Senft et al., 1987; Laca et al., 2010).

In this study, differences in body size of the large grazers could not account for habitat selection and use and therefore body size was not influential in fostering interspecific competition. Again, there was no relationship between body mass and grass quantity (grass biomass and percentage grass cover) or between body mass and grass quality (percentage digestible organic matter, percentage crude protein and percentage grass greenness); and the grazers showed poor or no clear pattern of habitat selection and use. High percentage digestible organic matter implies less fibre content of grass (forage) and low percentage digestible organic matter implies high fibre content. With high mean percentage digestible organic matter in all seasons it should be conclusive that forage in MNP generally had low fibre content, which therefore implied that larger grazers fed on forage in larger quantities (for their energy demands) than relatively small grazers; but this was not statistically significant. However, because of the low number of events for the percentage digestible organic matter and also for the percentage crude protein in respect of some of the habitat types, there should be caution in rejecting the hypothesis of interspecific decrease of forage quality or increase in forage quantity with increasing body mass.

Also, grass quality determined by percentage grass greenness did not influence the distribution and abundance of the two megagrazers (buffalo and elephant) but influenced either the distribution and/or abundance of all the

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relatively small-bodied grazers (kob, warthog and bushbuck) while only the waterbuck from the intermediate body-sized grazer group, including hartebeest and roan antelope were influenced by grass greenness. This observation supports the hypothesis of an allometric feeding strategy (Owen-Smith et al., 2010) as larger grazers were more likely distributed widely across the landscape of MNP as a means of acquiring sufficient forage to consume. It is therefore difficult to explain why grass biomass did not influence the distribution or abundance of the large-bodied grazers but this is probably because of the attempt to measure sufficient food in terms of grass biomass. A high frequency of small biomass can also make sufficient food requirement and this is probably the case for indiscriminate grazers. Whether percentage crude protein, percentage digestible organic matter, percentage grass greenness, percentage grass cover or grass biomass was high or low was not important for them as they grazed for sufficient forage to meet their energetic and nutritional food requirement. It is also difficult to explain why there was no significant relationship between body size and selectivity. This may also be due to indiscriminate selection that linked them to wide distribution on the MNP landscape with its fine scale mosaic to complicate any chance of identifying body size relationship with other variables. However, despite these anomalies it appears the megagrazers and intermediate body-sized grazers were less selective than their relatively small-bodied counterparts, in accordance with the allometric feeding hypothesis.

Though there was no significant seasonal relationship between body size and the other variables, it is suggested that the long fire season, during which

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there was indiscriminate burning of vast area of habitat, induced habitat shrinking. This presented challenging situations for the large grazers as they had to continue to select for optimal habitats. This could change the distribution of herbivores (Luzhang et al., 2005) through geographical shifts in species' ranges (Hu & Jiang 2011) that could reduce the future conservation value of PAs defined according to current herbivore populations and spatial requirements (Singh & Milner-Gulland 2011). Geographical shifts from MNP could be very devastating for the animals given reports of severe human-wildlife conflicts around the Park (WD, 2011).

Abundance and Distribution of the Large Grazers

The use of fire as a management tool in MNP and most African savannas plays a significant role in shaping grazer assemblages and in the structure and functioning of these ecosystems. It has been suggested that burning of savanna grasslands can have profound effects on the community structure of African herbivores due to differential preference for post-fire regrowth (Langevelde et al., 2003). The way savanna fires change vegetation structure and plant characteristics has been well studied but how this affects the communities of animals that consume these plants is completely unknown. Therefore, further studies on the effect of fire on mammalian assemblages will be necessary to provide useful information for the strategic application of fire as a management tool for promoting grazer assemblages. Until strict control of fire regimes become part of management agenda, fire will continue to present grazers with seasonal problems with habitat selection and use.

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Herbivores require access to several abiotic and biotic resources to carry out their biological functions (Parker et al., 2009) and this affects their distribution. In this study, it was found that distance to water and altitude were the most important abiotic variables as these affected the distribution or abundance of all the large grazers studied. All large grazers were always more abundant near water sources, and also always abundant at low altitudes except the hartebeest and buffalo. While the hartebeest were significantly more common at high altitudes, both abundance and distribution of buffalo were not significantly affected by altitude. The shift to areas near water sources and lowlands can constrain grazing use of some areas (Senft et al., 1987) so that some areas may be unexplored for foraging (Western, 1975; Redfern, Grant, Gaylard, & Getz, 2005) and all these contribute to the lack of clear patterns of distribution and abundance of the large grazers. The availability of only two water holes at MNP make water a limiting factor in the long dry and fire seasons and the mammals tended to concentrate around these few water holes during the study. Between the two influential variables, distance to source of water remains the only one that can improve.

Water development as a management practice has been used successfully to improve grazing distribution elsewhere (Valentine, 1947). Until water becomes seasonally and spatially available to the large grazers at MNP, it will remain impossible to see the importance of other abiotic and biotic factors in their distribution and abundance. However, biotic factors such as species composition, plant morphology, productivity, and forage quality and quantity are also known to affect grazing distribution and abundance (Bailey et al., 1996) as well. The trade-

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off between proximity to water and the availability of resources differs with species and landscapes (Redfern et al. 2005). Buffalo typically drinks every 1-2 days (Estes, 1991), but their size and mobility allow them to move further from water sources than relatively small body-sized species such as kob, warthog and bushbuck, despite their needing to drink only every 2-3 days (Estes).

Anthropogenic interference and disturbance have the potential to influence many aspects of herbivore ecology, particularly distribution and abundance. Herbivores under high hunting pressure often avoid areas close to human access points, such as communities and farms near the Park's boundaries (Laurance et al., 2006; Webb et al., 2011), and these make the variables, "distance to nearest community" and "distance to nearest boundary" very important. It appears that the large grazers most sensitive to anthropogenically-induced threats are the buffalo, roan antelope and hartebeest, which were absent from areas close to the Park's boundaries or the communities. This suggests some form of pressure inimical to these large-bodied grazers around the Park's boundaries and the communities.

Though the effect of predation on the abundance and distribution of the large grazers was not a subject in this study, it is an important factor because their prey are the subjects of this study. Predators at MNP, as far as large grazers are concerned, are lions, leopards and spotted hyaenas. The lions are most likely to contribute to substantial reduction of the large grazers' populations. Yet reports indicate there has been a significant decline in the lion population at MNP over the last 40 years (Burton et al., 2010) attributed to (i) a marked decrease in

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sightings by patrol staff, (ii) a lack of camera trap detections after a long survey period though other mammals including leopards and hyaenas were detected frequently, (iii) lack of evidence by spoors despite extensive field patrols, and (iv) no detections in call-in surveys and a sense of scarcity deduced from indigenous surveys (Burton et al., 2010). With such a heavy decline of the lion population, predation is expected to be too low to influence the abundance and distribution of the large-bodied large grazers (e.g. hartebeest, waterbuck, roan antelope and buffalo) at MNP; but the abundance and distribution of small-bodied large grazers (kob, warthog and bushbuck) could be affected by predation by leopards and hyaenas.

Therefore, this study supports the hypothesis of limiting factors, mainly water, fire and anthropogenic factors, imposing constraints on the abundance and distribution of large grazers. While all the three factors account for the lack of clear patterns of large grazer abundance, distribution and habitat selectivity, water and anthropogenic factors further make forage availability unexplored by the large grazers in most seasons.

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CHAPTER SIX: SUMMARY, CONCLUSIONS AND RECOMMENDATIONS

Summary

The effect of rainfall on grass at MNP was immediate, providing abundant and high quality forage for the large grazers. But because rainfall was followed by other seasonal events such as flood, dry and fire periods, there were seasonal variation in the quality and quantity of forage available to the large grazers and a cycle of alternating forage quality with quantity in which the rainy season provided high quality and the dry season high quantity. There was a resource stressed fire season for the large grazers but the fire event that preceded the rainy season became important for the refreshment of forage for the large grazers; thus this study supports the hypothesis that inferred that other factors acted in synergy with climate change to affect land cover changes, which affected large grazers in ways related to their habitat resource requirements.

There is currently an increase in populations of the large grazers and by evidence of a vast area of forage resources which remained unselected, MNP potentially has a carrying capacity that can sustain growing populations of the large grazers to a large extent.

The pattern of large grazers' selectivity and use of habitat resources in MNP has been complicated by biotic factors (including the fine-scale mosaic of habitats that characterize MNP and predation) and abiotic factors (including water, fire and anthropogenic factors). However, it is envisaged that improvement

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in such limiting factors can result in clear patterns of grazers' use of habitat resources. Clear patterns of habitat selectivity are very important for the construct and prediction of large grazers' distribution in MNP.

The large grazers responded to forage swelling in the rainy, flood and dry seasons by avoiding resource use overlaps, and this allowed no competition to occur; and responded to forage shrinkage in the dry season by allowing a degree of resource overlaps and competition among themselves.

High habitat diversity corresponds with high degree of species-packing and this allows species of similar sizes to co-exist. MNP has low species-packing because it has low species diversity. Like MNP, all the conservation areas in southern Africa compared defy the Hutchinson's co-existence rule as none of them had a degree of species-packing closer to the theoretically expected value of approximately 2.0 but there is co-existence of species of similar sizes. In MNP, this involved, mainly, species of small body weights. There also existed ecological holes due to the absence of species of similar body weights, especially in the large body weight category. The occurrence of ecological holes in the grazer assemblages at the MNP suggests the possibility of a successful translocation plan for (i) the giraffe which once lived there and (ii) Bohor reedbuck to augment its population; for the purposes of conservation of the species and tourism at MNP. It is also envisaged that proper management of water resources will increase co-existence of similar size species at MNP.

The hypothesis of interspecific decrease of food quality with increasing body mass was not supported by this study but there should be caution in rejecting

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it. This is because of the low number of sampling events for some of the variables. The sampling effort for the percentage digestible organic matter and percentage crude protein were particularly biased in respect of some of the habitat types. However, nutritional allometry was supported by this study as small-bodied large grazers were more selective in consuming high quality forage than large-bodied large grazers, which were more likely distributed widely across the landscape of MNP, feeding indiscriminately on resources with relatively low nutritional value.

Three limiting factors to habitat selectivity, species abundance and distribution of the large grazers observed by this study were water, fire and anthropogenic factors. Water was limited by the availability of only two water holes providing the water needs of the animals in MNP. Fire consumed a vast area of forage and anthropogenic factors imposed threats to the free distribution of the large grazers. Until there is improvement in the limitations of these three factors there cannot be any clear pattern of habitat selectivity, and species abundance and distribution.

There is currently no or minor competition among the large grazers of MNP. But there is a shift to a resource stressed condition in the fire season during which a degree of competition occurs. There is also a concern that because populations of these large grazers are increasing and the potential for their population growth enhanced by availability of resources, limiting factors will cause competition for resources among these sympatric grazer species by imposing restrictions to their selection and distribution processes.

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With the evidence of abundant forage resources, it is not unimaginable what the absence of such limitations, such as spatial availability of water all seasons, effective control of fire regimes and checks on anthropogenic factors, will bring to the large grazers. But in consequence, the large grazers are expected to select and use resources by preference instead of constraint and this will enable them to maximize their energy gain in the shortest possible time. This will reflect their real abundance and distribution patterns across seasons. In this case, resource overlaps will be minimal and competition further avoided. This may call for environmental manipulation of MNP.

The study of resource use overlap has been used to infer whether or not there is competition, nevertheless, it cannot be used in isolation. Other theories, more especially the weight ratio theory (species-packing) based on the Hutchinson's rule is also widely used to assess competition among grazers. Although the size ratio hypothesis has been sharply criticized for lacking a sound scientific base, it remains a useful descriptor of animal communities. It is noteworthy that though body size appears to be a useful measure for characterizing herbivore communities, it cannot be used to explain and measure diversity of large grazers in a community in isolation.

As a necessary measure for species conservation, it is very important for management of MNP to ensure that there is an optimal environment almost entirely free of constraints. This tends to construct the selective, abundance and

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distribution patterns that will properly define the behaviour of the large grazers on the MNP landscape.

Despite some limitations of the study, it successfully unraveled some important areas of the ecology of the large grazers that need to be considered in the formulation of a management plan for MNP and it is envisaged that the recommendations below will need attention for effective conservation action.

Recommendations

It can be inferred that the most important factor affecting the behaviour of the large grazers is water availability. However, water is available only in two water holes during the long dry and fire seasons. It is therefore recommended that as a foremost agenda, more water holes will be necessary and these should be placed strategically taking cognizance of habitat types, and spatial and altitudinal variations. Due to spatial distribution of habitats, water holes near boundaries of MNP will be necessary but if these are placed near staff camps or if the staff are deployed to be on duty at such water holes it would control poaching, possibly.

Since this study supported the need for fire as a management tool, burning of forage should continue to be encouraged. However, it is recommended that there is need to control fire regimes. It is suggested that since arbitrary fires result in forage shrinkage with adverse effect on forage availability, it will be better to strategize fire application to minimize shrinkage to have no or minimum adverse effect such as leading to competition. It will be ideal to plan how many areas of the same habitat type should be burnt in the same month, what total size of a

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particular habitat type should be burnt in the same month and how far away are areas being burnt at the same time. Burns should also take cognizance of the spatial distribution of each habitat type such as near or far away from boundaries. Ideally, for a particular fire month no habitat type should be burnt completely so that forage will always be available to explore in each habitat anytime.

Human dimensions of conservation have always been complex. However, the effect of anthropogenic factors on the assemblage of grazers could be reduced with patrols and monitoring. In this case the study revealed possible anthropogenic issues near the communities and boundaries of MNP and it is recommended that patrols and monitoring in these areas will be necessary to prevent poaching and to allow the large grazers free access to the forage there.

It is recommended that, for reliable results and conclusions, it would be ideal for this study to be replicated over two to five more years as it would be necessary to confirm the results by testing the significance of inter-annual variations over an extensive temporal scale.

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APPENDICES

Appendix A: Mean temperature and mean rainfall from 1980 to 2013

Year	Mean rainfall	Mean temperature
1980	88.2	26.8
1981	80.5	27.7
1982	72.4	29.3
1983	64.3	30.4
1984	89.3	28.1
1985	91.6	25.8
1986	89.4	26.2
1987	90.2	26.9
1988	88.4	27.3
1989	93.7	27.5
1990	87.6	27.2
1991	130.2	26.8
1992	136.1	26.8
1993	93.9	27
1994	83.3	26.9
1995	85.6	27.1
1996	85.8	26.9
1997	88.7	27.1
1998	79.2	27.7
1999	88.6	27
2000	102.2	26.7
2001	75.4	27.1
2002	96	27.2
2003	102.5	26.9
2004	103.8	27
2005	97.9	27.7
2006	92.4	27.5
2007	79.2	26.7
2008	90.8	27.3
2009	99.4	27.5
2010	117	26.4
2011	93.8	26.9
2012	97.6	27.4
2013	94.3	27.8

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Appendix B: Morisita's measure

BTV

	Elephant	Buffalo	Roan	Waterbuck	Hartebeest	Kob	Bushbuck
Elephant							
Buffalo	0.13						
Roan	0.28	0.08					
Waterbuck	0.07	0.01	0.03				
Hartebeest	0.23	0.11	0.53	0.09			
Kob	0.33	0.08	0.48	0.11	0.53		
Bushbuck	0.17	0.09	0.32	0.11	0.30	0.38	
Warthog	0.24	0.08	0.19	0.16	0.25	0.40	0.34

BTD

	Elephant	Buffalo	Roan	Waterbuck	Hartebeest	Kob	Bushbuck
Elephant							
Buffalo	0.09						
Roan	0.18	0.19					
Waterbuck	0.15	0.11	0.16				
Hartebeest	0.21	0.21	0.47	0.16			
Kob	0.28	0.07	0.08	0.20	0.27		
Bushbuck	0.40	0.08	0.05	0.17	0.25	0.60	
Warthog	0.39	0.08	0.04	0.35	0.20	0.38	0.39

Anogeissus

	Elephant	Buffalo	Roan	Waterbuck	Hartebeest	Kob	Bushbuck
Elephant							
Buffalo	0.37						
Roan	0.18	0.25					
Waterbuck	0.28	0.27	0.20				
Hartebeest	0.41	0.22	0.40	0.17			
Kob	0.38	0.23	0.19	0.33	0.33		
Bushbuck	0.27	0.26	0.22	0.28	0.15	0.54	
Warthog	0.30	0.36	0.17	0.20	0.23	0.40	0.40

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Appendix B, continued

	Elephant	Buffalo	Roan	Riverine Waterbuck	Hartebeest	Kob	Bushbuck
Elephant							
Buffalo	0.21						
Roan	0.03	0.00					
Waterbuck	0.32	0.08	0.08				
Hartebeest	0.08	0.04	0.10	0.29			
Kob	0.41	0.22	0.31	0.37	0.30		
Bushbuck	0.07	0.02	0.33	0.37	0.11	0.16	
Warthog	0.23	0.06	0.18	0.42	0.16	0.42	0.28

	Elephant	Buffalo	Roan	Swamp Waterbuck	Hartebeest	Kob	Bushbuck
Elephant							
Buffalo	0.00						
Roan	0.06	0.23					
Waterbuck	0.21	0.07	0.32				
Hartebeest	0.09	0.12	0.43	0.33			
Kob	0.38	0.07	0.09	0.25	0.26		
Bushbuck	0.15	0.15	0.07	0.26	0.06	0.55	
Warthog	0.35	0.10	0.06	0.30	0.28	0.31	0.39

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Appendix C: Results of regressing body mass against seven variables in the dry season at MNP

Variable	F-ratio	Degree of freedom	ρ
Area of habitat type	0.004	1, 640	0.950
Percentage greenness	0.251	1, 640	0.616
Grass biomass	0.195	1, 640	0.659
Nearest distance of grazer from Park's boundary	0.048	1, 640	0.828
Grazer distance from nearest community	0.799	1, 640	0.372
Grazer distance from nearest source of water	0.258	1, 640	0.612
Altitude	1.230	1, 640	0.268

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Appendix D: Results of regressing body mass against seven variables in the fire season at MNP

Variable	F -ratio	Degrees of freedom	ρ
Area of habitat type	1.046	1, 829	0.307
Percentage greenness	0.980	1, 829	0.322
Grass biomass	0.835	1, 829	0.361
Nearest distance of grazer from Park's boundary	0.031	1, 829	0.858
Grazer distance from nearest community	0.082	1, 829	0.775
Grazer distance from nearest source of water	0.663	1, 829	0.416
Altitude	0.003	1, 829	0.960

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Appendix E: Results of regressing body mass against seven variables in the rainy season at MNP

Variable	F-ratio	Degree of freedom	ρ
Area of habitat type	0.342	1, 635	0.559
Percentage greenness	0.154	1, 635	0.695
Grass biomass	0.433	1, 635	0.510
Nearest distance of grazer from Park's boundary	0.0001	1, 635	0.991
Grazer distance from nearest community	2.513	1, 635	0.113
Grazer distance from nearest source of water	0.183	1, 635	0.669
Altitude	0.001	1, 635	0.976

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Appendix F: Results of regressing body mass against seven variables in the flood season at MNP

Variable	F-ratio	Degree of freedom	ρ
Area of habitat type	1.197	1, 397	0.275
Percentage greenness	0.085	1, 397	0.770
Grass biomass	0.350	1, 397	0.554
Nearest distance of grazer from Park's boundary	0.001	1, 397	0.973
Grazer distance from nearest community	1.196	1, 397	0.275
Grazer distance from nearest source of water	0.070	1, 397	0.791
Altitude	0.382	1, 397	0.537

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