Effect of wildlife on forage selection by cattle (*Bos indicus* Lichtenstein) in a semi-arid environment, Kenya

By

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I dedicate this degree to my late mother, Felesia Atolwa Khanali, who devoted all her resources to my education and her dedication in prayer.

DECLARATION

I, **Moses Otiali Esilaba**, declare that this dissertation is my own work. The unpublished articles are the results of my own, original work and writing. Guidance and assistance were received from my supervisors to the extent usually and reasonably expected. The dissertation is submitted for the award of the degree of Doctor of Philosophy at the University of the Witwatersrand, Johannesburg and has not been submitted for any other degree or examination at another university.

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Abstract

Rangeland resources play a significant role in household production and sustainability of livelihoods among pastoral communities in Kenya. Although wildlife is one of the rangeland resources, it is viewed by pastoralists as a competitor with livestock for grazing resources rather than an economic resource. It is assumed that competition between wild herbivores and cattle may have an impact on the forage biomass in rangelands as well as on livestock production. It is from this view point of competition between wildlife and livestock for forage resources, that this study assessed effects of forage utilization by wildlife on cattle diet, plant community composition, forage biomass and level of forage utilization in semi-arid lands in Kenya. The following hypotheses were tested: there is a decline in proportion of dominant grasses due to wildlife grazing; there is a decline in forage biomass due to grazing by wildlife and there are changes in the diet of cattle (*Bos indicus* Lichtenstein) due to grazing by wild herbivores. Grazing experiments were conducted at the Kenya Long-term Exclosure Experiment (KLEE) on Mpala Ranch, Laikipia District, Kenya. A number of techniques were used during data collection: line transects and 1m^2 quadrats to assess plant species composition, richness and diversity. Forage biomass and increment in forage weight in grazed and ungrazed exclosures were determined by use of a disc pasture meter, whereas plant species consumed by cattle and wild herbivores were assessed by observation during feeding. The dietary forage composition of herbivores was done by micro-histological analysis of faecal samples of cattle, zebra, oryx, hartebeest and Grant's gazelle. The results indicate that there was a high (>21 %) proportion of the tall coarse grasses (*Pennisetum stramineum* and *P. mezianum*) in the exclosures grazed by cattle with wildlife in wet and dry seasons, whereas 21 % in the exclosures grazed by wild herbivores. The proportions of *Themeda triandra* in the exclosures grazed by cattle with wildlife in the dry season was 18 %, whereas it was more than 25 % in the exclosures grazed by cattle with wildlife in the wet season. The results also indicate that there were very highly significant ($p<0.0032$ and $p<0.0015$) differences in percentage composition of dominant and less dominant grasses between the grazed and ungrazed exclosures during the dry seasons, whereas a significant ($p<0.05$) difference and a highly significant ($p<0.01$) difference in percentage composition between the grazed and ungrazed exclosures during the wet seasons. 5 – 6 % of the total herbaceous forage biomass (0.7 % dry matter intake) was consumed in the exclosures grazed by wildlife, whereas 13 – 17 % (2.8 % dry matter intake) was consumed in the exclosures grazed by cattle. There was a large decrease of forage biomass in the pasture grazed by cattle. However, there was no significant ($p<0.133$) difference in forage biomass in exclosures grazed by large wildlife or grazed by elephants (mega-wildlife). There was less than 12 % utilization of dominant grass species in the exclosures grazed by wildlife, whereas over 40 % utilization of dominant grass species in the exclosures grazed by cattle. The results indicate that there is no evidence that grazing by wild herbivores decreases forage biomass in the pasture. Wildlife, therefore, should not be hunted out on communal grazing lands because it has no significant impact on the available forage biomass for livestocks. Nonetheless, stocking rates of livestock should be consistent with forage production so that wildlife conservation is integrated in pastoral production systems.

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CHAPTER ONE

Introduction

Background information

Competition between wildlife and livestock is of concern to livestock owners and scientific evidence for competition is scarce (Vavra *et al.* 1999). It is not clear whether wild herbivores grazing together with domestic livestock on the same piece of rangeland complement or compete for land or vegetation resource use (Ego *et al.* 2003). Generally, it is assumed that grazing and browsing by wild herbivores compete and deprive cattle of forage plants that are rich in nutrients (Ego *et al.* 2003). Deficiency of these nutrients in rangeland compels cattle to move in search of nutritious plants. During these movements, a lot of energy is spent resulting in low growth rates and low live weight gain that would adversely affect livestock production and have negative effects on the socio-economic wellbeing of the pastoral communities (Ego *et al.* 2003).

The competitive interactions between cattle and wildlife has been debated by ecologists (e.g. Murray & Illius 1996; Mishra *et al.* 2004; Owen-Smith 2002; Prins 2000) due to complexity in feeding patterns by herbivores, habitat and diet overlap and also resource partitioning. Interaction between herbivores is assumed to be competitive when a shared resource is limited and its use by two or more species results in reduced performance (e.g. survivorship, fecundity, or weight gain). Reduced cattle performance is associated with reduced forage intake and consumption of poor diet (Prins 2000). Competition may arise where species reduce shared food resources to levels below which they cannot be efficiently exploited by other species (Illius & Gordon 1992) and competition is unavoidable if there is overlap in habitat use and the resources are limited (Wiens 1989). Although indicative of potential for competition, overlap in observed patterns of resource use, whether high or low, does not necessarily imply anything about levels of competition in practice (Putman 1996).

Complementary feeding by large mammalian herbivores is exhibited by using forage resources that will rarely if ever be used by other mammalian herbivores. Specialist browsers like elephants are complementary to livestock in their use of their primary resources (Gordon *et al.* 2008; Riginos & Young 2007). Facilitation is deduced to occur if one species enhances performance of another species through improved food quality or intake via modification of the habitat (Arsenault & Owen-Smith 2002). Livestock has beneficial effects on wild ungulates through the redistribution of soil nutrients because native ungulates selectively used glades (bomas or temporary corrals) relative to surrounding nutrient poor habitats (Augustine *et al.* 2010).

Determination of competition among grazing herbivores requires an evaluation of resource use and experimental manipulation to demonstrate the occurrence of competition (Munday *et al.* 2001). A fundamental prediction of competition theory is a positive relationship between interspecific overlap in resource use (Munday *et al.* 2001 However, little information is known on impacts of forage utilization by wildlife on proportions of forage plants in a pasture, forage biomass or diet of cattle in semi-arid lands, thus knowledge gap exists. The purpose of this study was to carry out controlled replicated grazing experiments to investigate the effect of grazing by wildlife on forage biomass and to evaluate the effect of wildlife feeding on cattle diet. The findings of this study provide an insight into the impact of grazing by wildlife together with livestock on forage resources on communal grazing lands in Kenya and hence contribute to the existing knowledge on wildlife livestock interactions.

Forage is plentiful in the rainy season and immediately after rainy season but becomes scarce in the dry season, when some annual forage plants may disappear altogether (Herlocker 1979; Rutagwenda 1989). Various animals have evolved a range of mechanisms for coping with such fluctuations (Langer, 1988). Some select green high quality forage (Hofmann 1973; Kay *et al.* 1980) while others improve the digestion of poor forage by prolonging the retention in the fore stomach (Van Soest 1982; Van Soest *et al.* 1988). Foraging behaviour of herbivores provides the mechanistic link between animal species performance and the food in the environment (Owen-Smith 1994) and animal performance of grazing herbivores reflects forage quality which has an influence on forage intake (Newman *et al.* 2009). The spatio-temporal distributions of food items have been viewed as the dominant variables influencing foraging behaviour of wild herbivores (Owen-Smith & Novellie 1982).

Rangelands make up 87 % of Kenya's land area (Pratt & Gwynne 1977). These areas support over 25 % of the country's population, 52 % of the total livestock population and 90 % of the country's wildlife resources (Ottichilo *et al.* 2000; Matiko 2000). A large proportion of wild animal species in Kenya occurs outside as well as within protected areas (Maalim 2001) and outside protected areas wildlife share forage and water resources with livestock (Bergstrom & Skarpe 1999; Makombe 1993; Seno & Shaw 2002). However, there is a wide-spread belief by pastoral communities that wildlife compete with cattle for grass (Prins 1992, 2000; Voeten & Prins 1999).

Theoretically, sympatric herbivores with similar food habits will compete and those that have dissimilar food habits will not (Vavra *et al.* 1999). Nevertheless, it has been speculated that competitive interactions can be expected especially when grazing behaviour of animal species becomes similar (Van Wieren, 1996; Prins & Olff 1998) and information on feeding habits of pastoral animals is general (Odo *et al*. 2001). Although competition in the field is very hard to detect, evidence that it might be playing a role within grazer communities has been reported (Field 1972; De Boer & Prins 1990; Fritz *et al*. 1996; Prins & Olff 1998). The aim of this study was to assess impact of feeding by large wildlife on cattle diet in semi-arid lands in Kenya, and the objectives were to:

1. Determine the effects of grazing by cattle and wildlife on plant composition in semi-arid lands,
2. Examine wildlife and cattle feeding and forage utilization in semi-arid lands
3. Examine the response of plant biomass to grazing by wildlife and cattle in semi-arid lands and
4. Use faecal sampling to assess the effect of wildlife grazing on cattle diet in semi-arid lands, Kenya.

Study area

Mpala Research Centre is within Mpala Ranch, which is located in the central part of Laikipia District in Rift Valley Province, Kenya. Laikipia District is situated on the Equator, on the leeward side of Mt. Kenya. The district which covers 9175 km^2 lies between latitudes $0^\circ\ 18'$ S and $0^\circ\ 51'$ N and longitudes $30^\circ\ 11'$ E and $37^\circ\ 24'$ E. Mpala Research Centre lies at $0^\circ\ 17'$ N, $37^\circ\ 52'$ E and 1880 m above sea level. Mpala Research Centre is located on a 1200 hectare area on the 17000 hectare Mpala Ranch.

Climate

Mpala Ranch has an average annual rainfall of 500 to 600 mm. Two wet seasons (April-June and October-November) and two dry seasons (July-September and December to February) have been defined. The dry seasons receive less than 200 mm of rainfall. During the dry season, the day temperature is greater than 23 $^\circ$C and nights are cool with temperatures of about 13 °C. The humidity in the dry season is less than 10 % whereas there is 50 % humidity in wet seasons (Young *et al*. 2005).

Flora and fauna

The central part of Laikipia District falls within semi-arid lands (Heath 2000), with vegetation types composed of *Themeda-Pennisetum* grassland, *Acacia* bushland (containing *Acacia drepanolobium* Harms ex Sjostedt. and *Acacia seyal* Delile with *Themeda triandra* Forssk.), and leafy bushland (dominated by *Euclea divinorum* Hiern, *Carissa edulis* Vahl, *Searsia natalensis* (Bernh. Ex C. Krauss) F.A. Barkley. and *Tarchonanthus comphoratus* L.). Open thickets dominated by *Acacia brevispica* Harms and arid zone *Acacia* bushland dominated by *Acacia mellifera* Benth. and *Acacia nilotica* Benth. are commonly found on the well drained red soils in zone VI. The main vegetation type at the study site is bushed grassland with varying densities of *Acacia drepanolobi*um and *Acacia mellifera* Benth. Other woody species include *Cadaba farinosa* Forssk., *Balanites aegyptica* Wall. and *Searsia natalensis*.

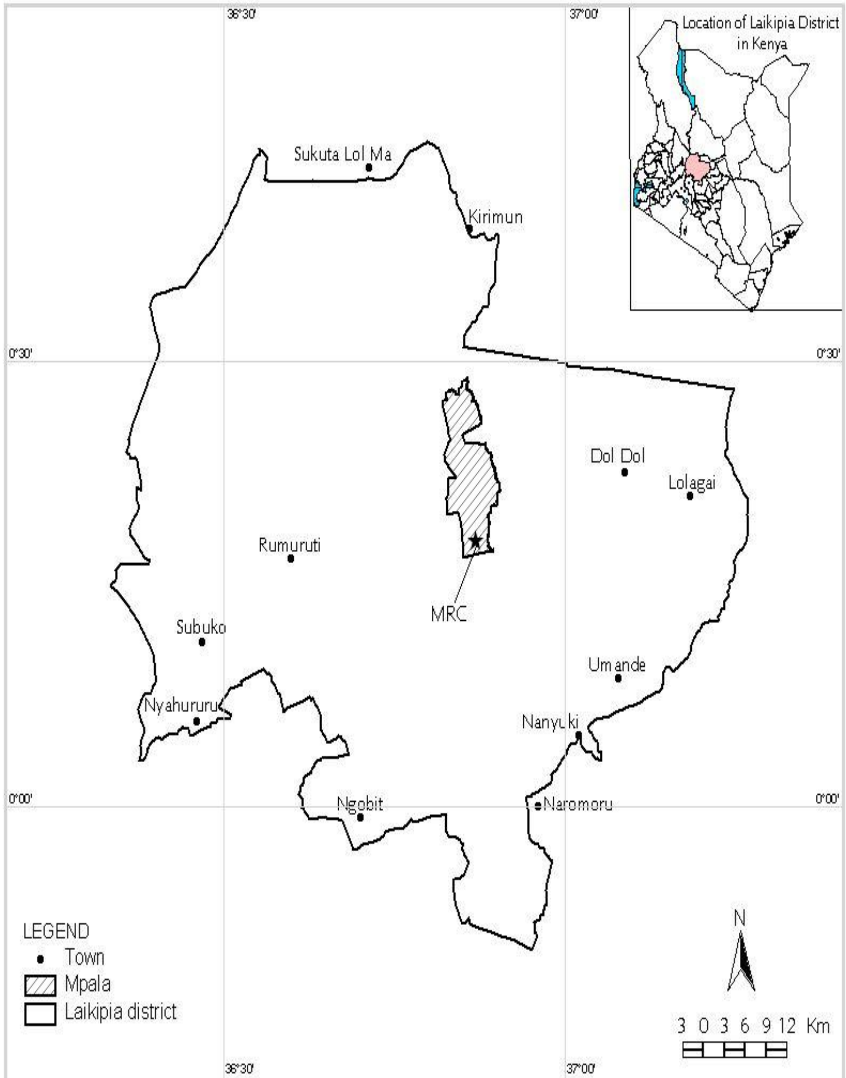

Figure 1. Location of Laikipia District and Mpala Research (MRC).

The herbaceous layer is dominated by perennial grasses, namely *Pennisetum stramineum* Peter, *Pennisetum mezianum* Leeke, *Brachiaria lachnantha* Stapf. and *Themeda triandra* Forssk., and several forbs including *Aerva lanata* Juss., *Aspilia pluriseta* Schweinf., *Solanum incanum* L., *Rhinacanthus ndorensis* Schweinf. ex Engl., *Dychoriste radicans* Rain. and *Commelina erecta* L. Further details about the vegetation of the study site are available in Young *et al.* (2005).

There are several mammalian herbivores, which include elephant (*Loxodonta africana* Blumenbach), giraffe (*Giraffa cameleopardalis* L.), plains zebra (*Equus burchelli* Gray), Grevy's zebra (*Equus grevyi* Oustalet), Grant's gazelle (*Gazella granti* Brooke), hartebeest (*Alcephalus buselaphus* Pallas), oryx (*Oryx beisa callotis* Ruppel), eland (*Taurotragus oryx* Pallas), buffalo (*Syncerus caffer* Sparrman) and steinbuck (*Raphicerus campestris* Thunberg). The carnivores include: spotted hyaena (*Crocuta crocuta* Erxleben), lion (*Panthera leo* L.) and leopard (*Panthera pardus* L.). Cattle (*Bos indicus* Lichtenstein) are the main livestock at the study site.

Experimental plots

The study was conducted in large herbivore exclosures, which consists of 18 exclosures (of 4 ha each) on three sites; South, Central and North with 6 exclosures on each site or block; that is, each treatment had three replicates (South, Central and North) on the same landscape. The exclosures are designated as follows: 1) O- Fenced to exclude all large herbivores; 2) C- Fenced, but cattle allowed to graze periodically; 3) WC- Electric fencing to exclude elephants and giraffes; 4) W- As in number 3, cattle excluded; 5) MWC- Unfenced, wildlife and cattle allowed to graze and 6) MW- Unfenced, cattle not allowed to graze (Fig. 2).

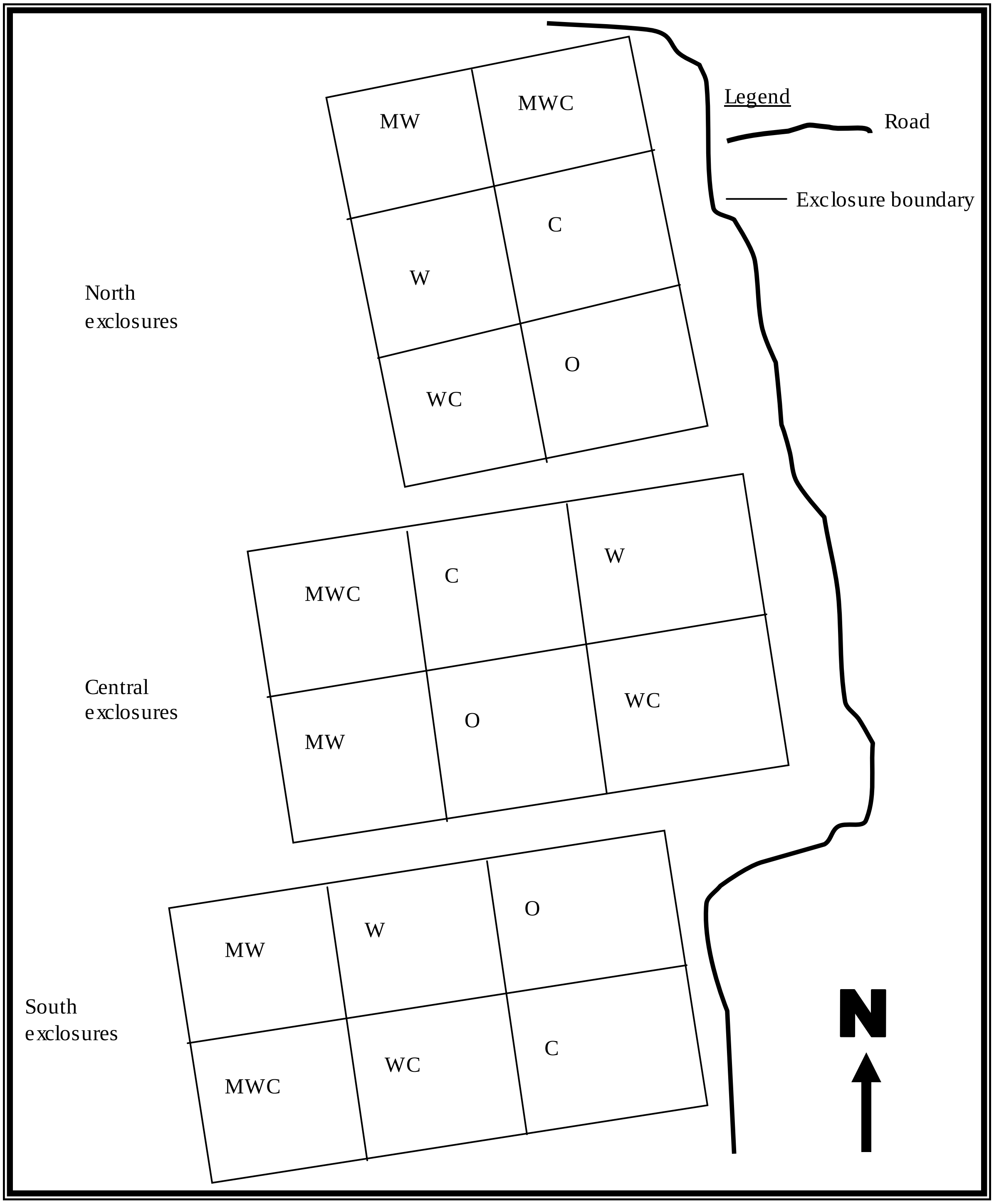

Figure 2. Schematic map of exclosures at Mpala Research Centre. Laikipia, Kenya. The letters in each exclosure indicate which herbivores are allowed: C- cattle; W- wildlife; M- mega-herbivores; O- all large herbivores excluded; WC- large wildlife and cattle allowed; MWC- all large and mega-herbivores allowed (Based on map in Young *et al* 2005).

The structure of the thesis

Chapter 1 provides a general introduction to the study and Chapter 2 determines impacts of large herbivores on plant community composition in semi-arid lands. Chapter 3 describes the effect of wildlife and cattle grazing on forage utilization in semi-arid lands, Kenya whereas chapter 4 examines the response of plant biomass to grazing by wild herbivores and cattle in semi-arid lands, Kenya. Chapter 5 describes the use of faecal sampling to assess the effect of wildlife forage preference on cattle diet in semi-arid lands, Kenya and Chapter 6 is the synthesis of the study by examining the competitive, facilitation and complementary interacions between cattle and wild herbivores on forage resources and the need to improve livestock production without compromising wildlife resources on communal grazing lands in Kenya.

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CHAPTER TWO

The impacts of herbivores on plant community composition in semi-arid lands, Kenya

Abstract

Change in plant species composition due to grazing is one of the indicators of rangeland condition and trend. Although studies may have been conducted in other regions of the world that looked at effects of grazing intensity on herbaceous forage plant species, no study has been conducted in Kenyan semi-arid lands that show impact of grazing by large wildlife on the herbaceous forage plant species, which may have long term effects on composition of plant communities and hence an effect on forage biomass. This study investigated the effects of cattle and wildlife grazing on botanical composition in the Kenya Long-term Experimental Exclosures (KLEE) at Mpala Research Centre, Laikipia District to determine herbaceous plant species composition, plant species richness and diversity in the exclosures. The data on botanical composition were collected in 1 m^2 quadrats laid at 100 sampling points along transect lines in grazed and ungrazed exclosures, and the plant species in the quadrat were identified and recorded. The percent frequency of grass and forb species was calculated and plant species richness and diversity was computed for each exclosure. Principal component analyses were used to estimate plant species richness and diversity as a result of cattle and wildlife grazing and a logistic regression model estimated the proportions of dominant grasses in exclosures grazed by cattle, wildlife and cattle grazing together with wild herbivores. The results show no evidence of change in the proportions of dominant grass species due to grazing by wild herbivores as there was no difference in the effects of large wildlife, megawildlife and cattle on proportions in the rangeland. Conversely, there was an increase in plant species richness and diversity in the exclosures due to cattle grazing but small variation on plant species richness and diversity in exclosures grazed by wildlife.

Therefore, wildlife should not be hunted out of communal grazing lands, instead the pastoral communities should incorporate wildlife in livestock production systems since wild herbivores have little effect on the composition of plant communities

Introduction

The role of herbivores in controlling plant species richness is a critical issue in the conservation and management of grazing systems (de Bello *et al*. 2007). Although the effects of grazing have been studied, little consensus has been reached with regard to grazing impact on grassland composition and productivity (Loeser *et al*. 2001). This study examined and evaluated the effect of moderate grazing by cattle and wildlife on the composition of plant communities and species diversity in a semi-arid environment.

Factors determining plant species composition in a pasture

Botanical composition of grassland communities is influenced by frequency of grazing, intensity and time of grazing by herbivores (Osem *et al*. 2002) so that grazing influences plant communities of grasslands but the extent of influence of grazing on botanical composition and diversity depends on the intensity of grazing (Kamau 2004). Grazing by livestock increases plant species richness in productive environments (Olff & Ritche 1998; Proulx & Mazunder 1998), but may cause decreases of plant species richness in habitats with low plant productivity, especially in arid regions (Olff & Ritchie 1998) (Fig. 3 s).

The effect of mammalian herbivory on composition of a plant community in a pasture

Herbivory is one of the major selective forces acting on plants (Crawley 1983; Huntly 1991). Selective grazing of individual plant species or species groups places them at a competitive disadvantage compared to less severely grazed species or groups and may thus alter competitive interactions and species composition within the community Briske *et al.* 2008). Intensive browsing by large wild herbivores reduces tree densities and increases herbaceous biomass (Young *et al.* 2005; Riginos & Young 2007; Goheen *et al.* 2007; Pringle 2008) by reducing leaf density and biomass of twigs and suppressing the growth of shrubs (Augustine & McNaughton 2004) (Fig. 3 a, b, g and h).

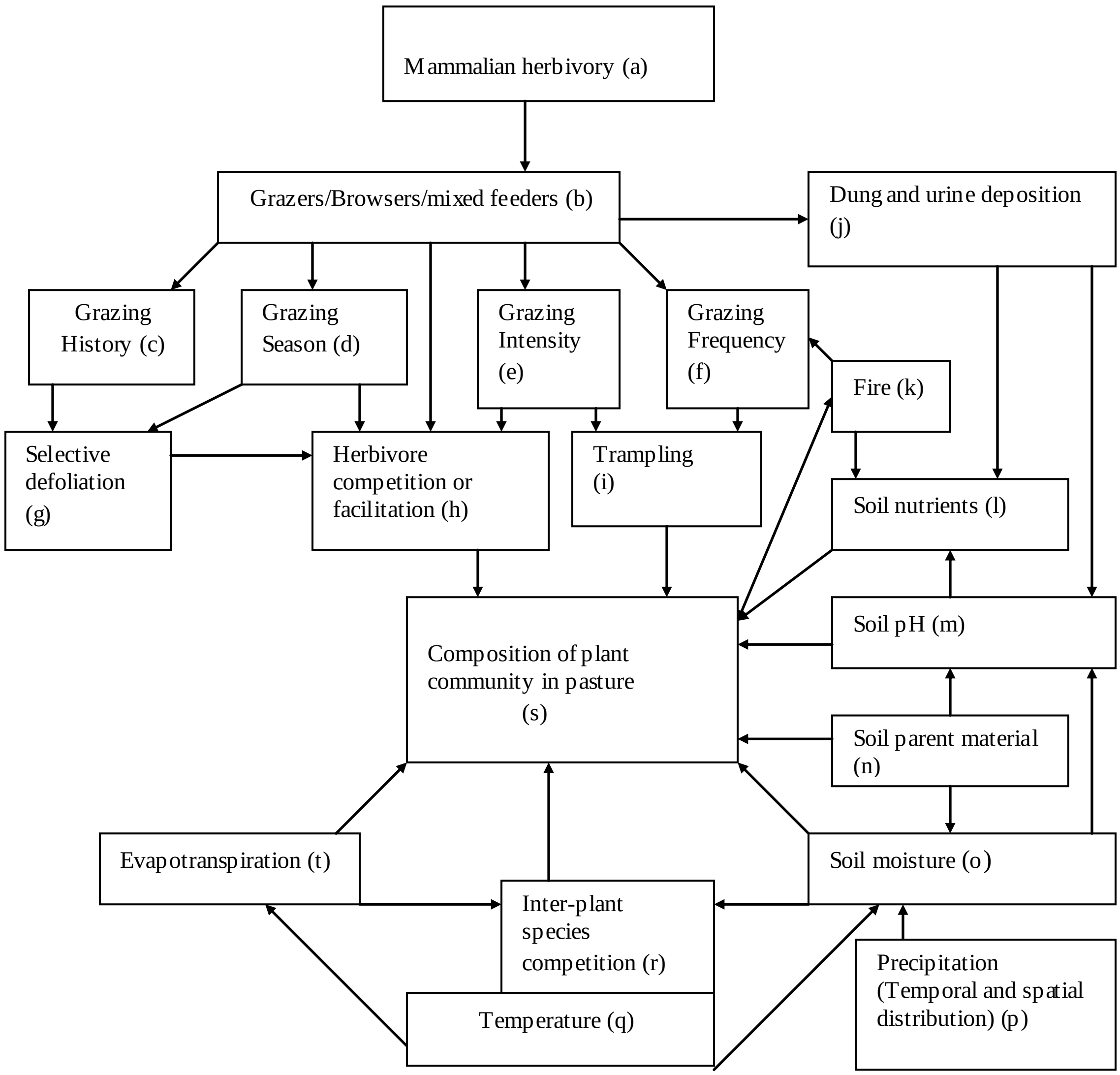

Figure 3. Factors that influence botanical composition of plant communities in a pasture.

The influence of history of grazing on composition of a plant community

Grazing history of the pasture is another significant factor influencing the botanical composition of any pasture (Oba *et al.* 2001). Herbivory can induce the expression of phenotypic variation of many traits which may lead to various phenotypes (and genotypes) being simultaneously present in a given area in contrast to a lower phenotypic variation present in ungrazed situations (van Wieren & Bakker 2008). There is no or very little variation in plant species with a short evolutionary history of grazing (van Wieren & Bakker 2008). Decreasers are reduced or eradicated, while increasers will gain a competitive advantage (Wheatley 2006) (Fig. 3 c).

The effects of grazing intensity, frequency, season and trampling on the composition of a plant community

Frequency of grazing has an impact on plant species composition of a pasture. Under continuous grazing, herbivores constantly remove leaves of plants and this does not allow the replenishment of root reserves, thus diminishing the competitive ability of desirable plants and encouraging undesirable plants (Andrae 2004). Although trampling results in breakage of plants which affect water infiltration into the soil (Chaichi *et al.* 2005), trampling breaks soil crusts and improves infiltration (Fig. 3 d, e, f and i).

The influence of soil types and nutrient cycling on the composition of a plant community

Soils, topography, time, vegetation and microbes may have a localized effect on rangeland vegetation (Herlocker 1999). Variability of soil characteristics may result in distinctive sites, which have characteristic vegetation types (Wells & Dougherty 1997). Livestock and wildlife may increase soil fertility through nutrient recycling by dung and urine deposition, accelerating the nitrogen mineralization rate (Afzal & Adams 1992; Russelle 1992; McNaughton *et al.* 1997; Rotz *et al.* 2005) which increases nutrient availability for the regrowth of grazed plants (Semmartin & Oesterheld 2001)(Fig. 3 j, l, m, and n).

The influence of precipitation, soil moisture and temperature on the composition of a plant community

Rainfall is the principal factor that influences vegetation community composition in semi-arid lands. The low annual rainfall that averages 250 – 600 mm per annum in arid and semi-arid lands is erratic and unreliable (Herlocker 1999) and may impact plant species composition and diversity. Effects of biotic factors such as grazing on plant community structure and biomass may be masked by the variation in amount of rainfall (Ward 2004). However, occurrence of specific plant species in an ecosystem is affected by the annual precipitation (Jones 1995), which in turn, influences the soil moisture (Scott & Maitre 1998) and the botanical composition on a range site. Temperature in semi-arid lands is seldom a limiting factor to plant growth (Lind & Morrison 1974; Pratt & Gwynne 1977), but high temperatures in semi-arid lands may increase evapotranspiration, thus affecting plant species richness and diversity (Herlocker 1999) (Fig. 3 o, p, q and t).

The influence of fire on the composition of a plant community

One of the most important reasons for burning grasslands and savanna vegetation in Africa involves the removal of moribund and or unpalatable grass material to improve quality of the grazing for domestic stock and wildlife (Tainton 1999; Trollope 2011). Previously, fire may have influenced plant species but due to suppression of fire by Mpala managent, effects of fire on plant communities are minimal at study site (Augustine 2003) (Fig. 3 k).

Studies have been carried out in semi-arid lands of Kenya to determine the impact of livestock grazing on botanical composition (Sitters 2009; Goheen *et al.* 2007; Kamau

2004; Oba *et al*. 2001) but no controlled experiments have been conducted in the semi-arid lands in Kenya to assess the impact of wildlife grazing on proportions of herbaceous plant species and so there is a knowledge gap about the effects of livestock and wildlife grazing together on plant species composition in a pasture.

Materials and methods

Grazing trials

One hundred Boran heifers weighing between 250 and 300 kg were introduced in each of the fenced exclosures in which only cattle are allowed to graze periodically (C), exclosures with electric fencing to exclude elephants and giraffes but cattle and large wildlife allowed (WC) and unfenced exclosures in which cattle, large wildlife, elephants and giraffes are allowed to graze together (MWC) (Fig.2). The Boran cattle were introduced in the C, WC and MWC exclosures during the second week of November 2007, February 2008 and June 2008 and grazed between 08.00 hrs to 12.00 hrs once. The stocking density in the exclosures was 0.14 livestock units per hectare (7 ha/livestock unit) per year based on the duration of grazing of four hours a day and three times a year in the exclosures. This stocking density was within the recommended moderate stocking density of 0.16 – 0.12 livestock unit per hectare (6 – 8 ha/livestock unity) by Mpala Research Centre management, but less than the recommended stocking rate of 0.26 livestock units/ha (4 ha/livestock unit) on semi-arid lands in Kenya (Pratt & Gwynne 1977). However, there was free access of large wildlife into the exclosures grazed by large wildlife alone (W), large wildlife, giraffe and elephant (MW), cattle and large wildlife (WC) and cattle, large wildlife, giraffe and elephants (MWC). The free acess by wildlife into exclosures was because wild herbivores could not be controlled in the same way as cattle thus there was a higher stocking density in WC and MWC compared to C exclosures. Although wildlife stocking density was not measured at the KLEE during the study, the total stocking rate in WC and MWC exclosures was likely to be over 0.144 and 0.2 livestock units per hectare compared to estimated densities of 0.004 ± 0.002 (SE) and 0.05 ± 0.01 livestock units per hectare per year of megaherbivores and medium-sized wild herbivores in Laikipia District based on aerial surveys conducted between 1985 and 2003. The high-intensity-short-duration (HISD) grazing by cattle, followed by deferment, was to provide an opportunity for grazed plants to recover in growth and nutrient cycling between grazing cycles (Hall 2004). Although moderate cattle stocking density was used in the exclosures grazed by cattle, the results obtained in the exclosures grazed by cattle together with wildlife (WC and MWC) can be used to predict changes in the proportion of plant species composition, plant species richness and diversity on communal grazing lands on which large numbers of livestock and wildlife share forage resources.

Plant species identification

In each exclosure, sampling points were marked at 10 m intervals along a 100 m transect. A 1 m^2 quadrat was laid at each sampling point and the plant species within the quadrat were identified to species level and recorded, while plants that were not easily identified were identified through comparison with preserved plant specimens in the herbarium at Mpala. Mpala Research herbarium has a collection of all the plant species found on Mpala Ranch, which were collected during the collection of baseline data and identified in collaboration with the Herbarium of the National Museum of Kenya and Smithsonian Institution.

Determination of herbaceous plant species composition

Composition of herbaceous plants was assessesd by use of quadrats (1 m^2) which were laid out at sampling points ten metres apart along ten transect lines, i.e. measurements were taken at 100 sampling points in each exclosure. At each sampling point, plant species within the 1 m^2 quadrat were identified and recorded.

Frequencies of herbaceous plant species in each exclosure were determined by the formula:

$$f = \frac{\text{number of points at which plant species occurred}}{\text{Total number of points examined}} \times 100$$

where f is the frequency percentage of each plant species.

Grass cover

Herbaceous (grasses and forbs) vegetation cover was determined by point-frame, which was placed within the 1 m^2 quadrats. The ten pins on the point-frame were lowered and the canopy of the plant species touched by each pin was recorded. The total number of hits of each species in 100 sampling points in an exclosure was converted to percentage cover. The percentage cover of each species per transect was determined by the formula:

$$\text{Percent cover}_{sp} = \frac{\text{Hits}_{sp} \times 100}{1000}$$

where percent cover_{sp} = percent cover of a species on a transect

Hits_{sp} = the number hits of a species

1000= total number of pins in 100 points in an exclosure.

Species diversity

a). Alpha diversity (α) refers to the average number of species found in a set of sample units or areas (Veech *et al.* 2002). It can be described as species richness (Nieppola 1992).

The determination of alpha diversity in each exclosure was by the following formula:

$$\alpha = \frac{\text{total number of plant species encountered in all sampling points}}{\text{Total number of sampling points}}$$

where α is the alpha diversity, which is the mean plant species per sampling point (1 m^2 quadrat).

The measurements of the plant species richness (alpha diversity) were taken during the 2007 wet, 2008 dry and 2008 wet seasons (in November, February and June respectively), in the 18 exclosures on the south, central and north at the study site (KLEE). Number of grasses, forbs and shrubs in the sampling plots (quadrats) were counted, recorded and mean number of plants per quadrat in each exclosure was computed for the wet and dry seasons. Principal Component Analysis was done to determine influence of grazing and season on alpha and beta diversity in exclosures. The assumption made was that there were linear relationships between the plant species richness, species turn-over and grazing intensity and season.

The beta species diversity in each exclosure was determined by dividing all the plant species encountered in all exclosures (gamma diversity (γ)) by mean alpha diversity (α) per quadrat. Beta diversity was calculated as the ratio of gamma diversity (total diversity) and alpha diversity (within habitat) (Descrochers & Anand 2004; Ricotta 2005), i.e. $\beta = \frac{\gamma}{\alpha}$

where α, β and γ are alpha, beta and gamma diversities respectively.

Principal Component Analysis was undertaken to show the relationships between season and intensity on the species-turn over (changes in species composition).

Density of woody species

A number of studies on density of woody species in the exclosures have been conducted and the data are available (e.g. Riginos & Grace 2008; Goheen *et al.* 2007; Pringle 2008). The results of a baseline study by Young *et al.* (1998) at the study site show that the overstorey is dominated by *Acacia drepanolobium* that accounts for over 97 % with mean density 2267 ha^{-1}. Other woody species such as *Cadaba farinosa, Searsia natalensis, Acacia mellifera, A. brevispica, Balanites sp., Boscia sp.* and *Lippia javanica* occur in the plots, but at low densities and account for 2.3 % of the woody species.

Another study was conducted by Augustine *et al.* from 2004 to 2007 period that assessed changes in the size of *A. drepanolobium* in exclosures with all large herbivores were excluded and exclosures to which all large herbivores had access. All *A. drepanolobium* trees were counted in two 150 x 50 m strip transects each year. The results indicated that large herbivores reduced density of *A. drepanolobium* by 32 % and canopy cover by 28 % and woody biomass by 29 %. Therefore, the results demonstrate that browsers strongly influence woody vegetation dynamics (Augustine *et al.* 2010). In a similar study in the exclosures reproductive status of *A. drepanolobium* was determined by recording the presence of fruit, height, stem circumference, crown diameter and occupancy of *Crematogaster sjostedti* Mayr or *Crematogaster Mimosa* Santschi (Goheen *et al.* 2007). A total of 1914 *A. drepanolobium* trees were recorded in all the plots. The results indicated high tree density in exclosures without wild herbivores and low tree density in exclosures in with wildlife had access. Therefore, the results demonstrate that the presence of browers in arid and semi-arid lands reduce tree density that may lead to an increase in cover of herbaceous layer.

Transformation of the proportions of the dominant grasses

The percentage frequency of *Brachiaria lachnantha*, *Pennisetum stramineum*, *Pennisetum mezianum*, *Themeda triandra*, *Lintonia nutans* and *Bothriochloa insculpta* in the 100 1m^2 quadrats in the exclosures grazed by large wildlife (W), large and mega-wildlife (MW) and cattle with wildlife (MWC) were converted into ratio of proportions (p) and the data transformed into log-odds; i.e. $\hat{Y} = \log\left(\frac{p}{1-p}\right)$ (Dayton 1992) of a particular grass species. The log-odds values were used in logistic regression to examine the effect of herbivore type and season on the proportions of the dominant grass species. These dominant grasses were selected because they provided the bulk of forage to the herbivores. The impact of wildlife and cattle grazing on grass species in the pasture was determined using a loglinear model:

$$\hat{Y} = w + m + c + y + s$$

where $\hat{Y}$ is the log-odds of grass species in the exclosures (dependent variable); “w” indicate the presence of large wildlife in the exclosure; “m” indicates presence of mega wildlife in the exclosures; “c” indicates the presence of cattle in the exclosure; “y” indicates the year (2007 and 2008) when measurement was undertaken; “s” indicates the wet or dry season when the measurement was taken (independent variables). The transformation of the data into log-odds was to meet the assumptions for the linear models.

The presence or absence of large wildlife, mega-wildlife and cattle were coded as 1 and 0 respectively and the codes were used in the regression analysis. Statistical Package for Social Sciences (SPSS) version 11.5 computer software was used in the linear regression analysis of independent variables (m+w+c) against the log-odds of the grasses in MWC exclosures (dependent variable). The inverse of the log (anti-log) values of the coefficients of the estimates of the best fit regression line; i.e. $e^{(\hat{Y})}$ were used to calculate the estimates of the proportions of grass species due to grazing by wildlife and by cattle.

Data analysis

Descriptive statistics were applied (using STATISTICA computer software, version 6), to compute means of percentage frequencies, whereas Analysis of Variance (ANOVA) was used to determine the difference in means of percentage frequencies of grasses and forbs among the exclosures. The ordination of alpha and beta species diversity to determine the correlations between plant richness (alpha-diversity), plant species turn-over (beta-diversity) and grazing intensity and seasons (rainfall) was done using Principal Component Analysis (PCA). Logistic regression analysis was done using SPSS computer software whereby the log odds in ungrazed exclosures and of each herbivore (independent variables) were entered and the coefficients (β) generated by the regression model for the ungrazed (constant), wildlife and cattle grazing recorded. The anti-log of the coefficients were used to determine the proportions of dominant grasses in the exclosures due to grazing by wild herbivores and cattle.

The actual proportion of each grass species was determined using the following formula:

i.e. $x = \left(\frac{p}{1-p}\right)$; $x - xp = p$

$$x = p + xp$$

$$x = p + xp$$

$$\frac{x}{1 + x} = p$$

where: x is the $e^{(\hat{Y})}$ value and p is the proportion of dominant grass species due to grazing by cattle and wildlife in the exclosures

Results

Plant species composition in the exclosures

The composition of herbaceous plant communities at Kenya Long-term Exclosure Experiment (KLEE) consisted of perennial and annual grasses and forbs. Twenty-three grass species (34 %) and forty-seven forbs (66 %) were identified. Although there were more species of forbs than grasses, the grasses were more dominant and formed 80 % of plant species cover of the pasture. The grasses were grouped into two categories dominant (>10 % frequency) and less dominant (1 – 10 % frequency). The dominant grass species included: *Brachiaria lachnantha, Pennisetum stramenium, P. mezianum, Themeda triandra, Bothriochloa insculpta* and *Lintonia nutans* whereas *Digitaria milanjiana, Sporobolus festivus, Eragrostis tenuifolia, Brachiaria eruciformis, Aristida congesta* and *Dinebra retroflexa* were less frequent. A dominant grass-like plant in exclosures was *Cyperus elatus*. The dominant forbs were *Aerva lanata, Aspilia pluriseta, Monechma debile, Pseudognaphalium declinatum, Dyschoriste radicans, Commelina erecta* and *Rhynchosia nyasica*.

Rainfall distribution

The exclosures received high rainfall during the short rainy season (October to December) and less amounts in the long rainy season (April to August) in 2007 and 2008. However, the 2007 wet season had the highest amount of rainfall compared to 2008 (Fig.4). 2008 had the highest range (4.3 – 138 mm) of rainfall during the short rainy season and lowest range (4.5 – 57 mm) during the long (April – August) rainy season. 2007 and 2008 dry seasons had a small range (0 – 11.6 mm and 2 – 19.4 mm) of rainfall. The rainfall amounts were measured every week and recorded for three months in October-December short rains and January-March dry season, whereas during the long rainy season the rainfall measurements were recorded for five months. The amount of rainfall had an influence on plant species composition and hence biomass in the exclosures as indicated by the results in figures 5 – 7 and results on forage biomass in Chapter 4.

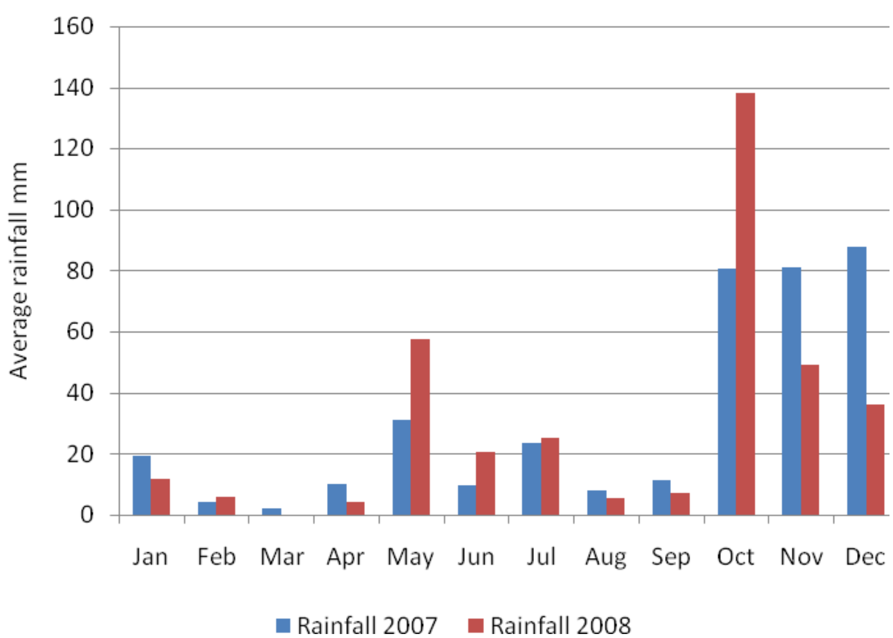

Figure 4: Variation in mean monthly rainfall recorded in the exclosures (study site).

The logistic regression model (Table 1) shows the estimated proportions of dominant grass species in the pasture due to grazing by large wild herbivores (w), mega-wild herbivores (+m) and cattle (+c). Generally, there were decreases in the proportions of the dominant grasses due to grazing by herbivores. There were 7 % and 9 % less in the proportions of *Pennisetum stramineum* and *P. mezianum* due to grazing by large and mega-wildlife compared with proportions in the ungrazed pasture, whereas less than 7 % in the proportions due to grazing by cattle compared to ungrazed pasture. Conversely, there was 3 – 6 % less in the proportions of *Brachiaria lachnantha*, *Themeda triandra, Lintonia nutans* and *Bothriochloa insculpta* due to grazing by wildlife and cattle compared to ungrazed pasture in the 2007 wet season. The results indicate a high decrease in the proportions of tall coarse grasses due to grazing by wildlife compared to grazing by cattle in the 2007 and 2008 wet seasons. However, in the 2008 dry season cattle grazing greatly affected the proportions of *Brachiaria lachnantha, P. mezianum* and *Themeda triandra* with 9 %, 11 % and 7 % less in the proportions compared with ungrazed exclosures. Similarly mega-wildlife had greatest effect on the proportions of *P. mezianum* with 11 – 12 % less in the proportions compared with ungrazed pastures. In contrast, grazing by wild herbivores and cattle had least effect on the proportions of *Lintonia nutans* and *Bothriochloa inscuplta* with <4 % decrease in the proportions in the wet and dry seasons.

Table 1: Estimates of the proportions of dominant grass species due to grazing by large wildlife, mega-wildlife and cattle in the exclosures (L=lower limit, U= upper limit at 95 % confidence interval: calculated by 2 x SE). SE=standard error. The reference is ungrazed exclosure (constant).

Season/grass species/ herbivore type 2007 wet season *Brachiaria lachnantha*	Coefficient (β)	SE	95 % CI Bl (L)	Bl (U)	% estimates of the proportions of grasses due to grazing	Df	F	T	Sign	R^2
Constant	-1.045	0.845	-2.735	0.645	26	99	28.053	-1.317	0.068	
W	-.1.380	0.183	-1.746	-1.016	20			-4.194	0.0001	.431
+ m	-1.339	0.682	-2.703	0.025	21			-3.470	0.0001	
+ c	-1.186	0.372	-1.930	-0.442	23			-3.162	0.0001	
Pennisetum stramineum			Ps (L)	Ps (U)						
Constant	-0.967	0.770	-2.508	0.569	28	99	66.461	-1.694	0.110	
W	-1.355	0.611	-2.577	-0.113	21			-5.166	0.0001	.726
+ m	-1.310	0.334	-1.978	-0.642	21			-3.286	0.0001	
+ c	-1.246	0.604	-2.454	-0.038	22			-7.294	0.0001	
Pennisetum mezianum			Pm (L)	Pm (U)						
Constant	-0.841	0.835	-2.511	0.829	30	99	71.058	-0.630	0.174	
W	-1.340	0.622	-2.584	-0.096	21			-9.295	0.0001	.793
+ m	-1.305	0.619	-2.543	-0.068	21			-9.730	0.0001	
+ c	-1.072	0.389	-1.850	-0.294	26			-7.178	0.0001	
Themeda triandra			Tt (L)	Tt (U)						
constant	-1.057	0.538	-2.133	0.019	26	99	37.210	-3.687	0.129	
W	-1.259	0.419	-2.097	-0.421	22			-7.283	0.0001	.576
+ m	-1.215	0.341	-1.897	-0.533	23			-3.701	0.0001	
+ c	-1.319	0.389	-2.097	-0.541	21			-2.842	0.015	

Lintonia nutans			Ln (L)	Ln (U)							
Constant	-1.153	0.538	-2.229	-0.077	24	99	58.341	-1.367	0.287		
W	-1.362	0.475	-2.312	-0.412	20			-8.371	0.0001	.676	
+ m	-1.420	0.405	-2.230	-0.610	20			-9.901	0.0001		
+ c	-1.395	0.858	-3.111	0.321	20			-4.826	0.0001		
Bothriochloa insculpta			Bi (L)	Bi (U)							
Constant	-1.125	0.816	-2.757	0.507	25	99	38.185	-1.173	0.087		
W	-1.230	0.380	-1.990	-0.470	23			-6.067	0.0001	.570	
+ m	-1.207	0.405	-2.017	-0.397	23			-5.931	0.0001		
+ c	-1.262	0.858	-2.978	0.454	22			-3.152	0.0001		
2008 dry season											
Brachiaria lachnantha			Bl (L)	Bl (U)							
Constant	-0.852	0.743	-2.338	0.634	30	99	41.381	-1.951	0.167		
W	-1.113	0.309	-1.731	-0.495	25			-5.419	0.0001	.639	
+ m	-1.063	0.434	-1.931	-0.195	26			-7.184	0.0001		
+ c	-1.350	0.338	-2.025	-0.648	21			-3.251	0.0001		
Pennisetum stramineum			Ps (L)	Ps (U)							
Constant	-1.028	0.671	-2.370	0.314	26	99	78.973	-3.003	0.048		
W	-1.319	0.487	-2.293	-0.345	21			-11.608	0.0001	.752	
+ m	-1.463	0.358	-2.179	-0.747	19			-13.840	0.0001		
+ c	-1.275	0.306	-1.887	-0.663	22			-9.503	0.0001		
Pennisetum mezianum			Pm (L)	Pm (U)							
Constant	-0.694	0.645	-1.984	0.596	33	99	41.466	-1.843	0.071		
W	-1.170	0.497	-2.164	-0.176	23			-6.184	0.0001	.715	
+ m	-1.260	0.358	-1.976	-0.544	22			-4.093	0.0001		
+ c	-1.001	0.556	-2.113	0.111	26			-3.375	0.001		

Themeda triandra			Tt (L)	Tt (U)						
Constant	-0.914	0.849	-2.612	0.784	29	99	26.280	-2.127	0.069	
W	-1.019	0.295	-1.609	-0.429	26			-7.271	0.0001	.472
+ m	-1.003	0.347	-1.697	-0.309	27			-5.821	0.244	
+ c	-1.538	0.260	-2.058	-1.018	18			-3.072	0.015	
Lintonia nutans			Ln (L)	Ln (U)						
Constant	-1.108	0.878	-2.864	0.648	25	99	71.740	-2.623	0.186	
W	-1.225	0.394	-2.013	-0.437	22			-10.114	0.0001	.739
+ m	-1.260	0.397	-2.054	-0.431	22			-7.295	0.0001	
+ c	-1.348	0.608	-2.564	-0.132	20			-5.351	0.0001	
Bothriochloa insculpta			Bi (L)	Bi (U)						
Constant	-1.327	0.615	-2.557	-0.0.97	21	99	119.60	-2.038	0.248	
W	-1.250	0.399	-2.048	-0.452	22			-12.284	0.0001	.839
+ m	-1.304	0.446	-2.196	-0.412	21			-6.477	0.0001	
+ c	-1.385	0.390	-2.165	-0.605	20			-9.329	0.0001	
2008 wet season										
Brachiaria lachnantha			Bl (L)	Bl (U)						
Constant	-1.127	0.472	-2.071	-0.183	24	99	79.196	-2.716	0.063	
W	-1.341	0.435	-2.21	-0.469	21			-8.940	0.0001	.789
+ m	-1.263	0.385	-2.033	-0.493	22			-12.184	0.0001	
+ c	-1.410	0.319	-2.048	-0.772	20			-6.972	0.0001	
Pennisetum stramineum			Ps (L)	Ps (U)						
Constant	-1.038	0.515	-2.068	-0.008	26	99	110.16	-3.126	0.025	
W	-1.390	0.531	-2.452	-0.328	19			-22.284	0.0001	.815
+ m	-1.461	0.533	-2.527	-0.395	18			-20.602	0.0001	
+ c	-1.163	0.461	-2.085	-0.241	24			-7.918	0.000	

Pennisetum mezianum			Pm (L)	Pm (U)						
Constant	-1.060	0.641	-2.342	0.222	26	99	51.271	-1.396	0.168	
W	-1.332	0.479	-2.290	-0.374	17			-10.028	0.0001	.641
+ m	-1.385	0.517	-2.419	-0.351	20			-6.266	0.0001	
+ c	-1.096	0.540	-2.176	-0.016	25			-2.703	0.007	
Themeda triandra			Tt (L)	Tt (U)						
Constant	-1.109	0.631	-2.371	0.153	25	99	97.258	-1.399	0.0216	
W	-1.164	0.430	-2.024	-0.304	23			-11.650	0.0001	.733
+ m	-1.271	0.383	-2.037	-0.505	22			-10.183	0.0001	
+ c	-1.315	0.414	-2.143	-0.487	21			-1.725	0.001	
Lintonia nutans			Ln (L)	Ln (U)						
Constant	-1.124	0.614	-2.352	0.104	25	99	68.941	-1.580	0.263	
W	-1.280	0.493	-2.266	-0.294	22			-10.082	0.0001	.731
+ m	-1.255	0.413	-2.081	-0.429	22			-8.195	0.0001	
+ c	-1.371	0.815	-2.587	-0.155	20			-7.571	0.0001	
Bothriochloa insculpta			Bi (L)	Bi (U)						
Constant	-1.581	0.741	-3.063	-0.099	17	99	31.317	-2.269	0.247	
W	-1.530	0.493	-2.516	-0.544	18			-6.710	0.0001	.692
+ m	-1.475	0.390	-2.255	-0.695	19			-5.926	0.0001	
+ c	-1.226	0.454	-2.134	-0.318	23			-4.715	0.0001	

w = the estimated percentage proportions in the exclosures due to grazing by large by wildlife (e.g. zebra, oryx, gazelles, hartebeest); + m = proportions in the exclosures due to grazing by mega-wildlife (elephants and giraffes); + c = proportions in the exclosures due to grazing by cattle

Multivariate analysis of plant species diversity

Alpha diversity

The strength of correlation between the response of alpha diversity (dependent variable) to grazing herbivore type and rainfall (independent variables) is indicated by the percentage of the total variance of axes on the ordination plot. High percentages of the total variance of the axis indicate a strong association between the independent and dependent variables and the longer the arrow the stronger the association. The positive correlations indicate that plant species richness increased with the herbivore type grazing or rainfall, while negative correlations indicate that species richness decreased with herbivore type or rainfall (Fig.5).

There were strong positive correlations between alpha diversity measured in November (α-N), and cattle grazing (C), and amount of rainfall in the 2007 wet season, while there were weak correlations between June alpha diversity (α-J) and C, MW and amount of rainfall in the 2008 wet season. There were also strong positive correlations between February alpha diversity (α-F) and cattle grazing together with large and mega-herbivores (MWC), while a weak correlation between α-F and large wildlife and cattle grazing together with large wildlife (W and WC). However, there were negative correlations between amount of rainfall in the dry season and the α-N and α-J species diversity.

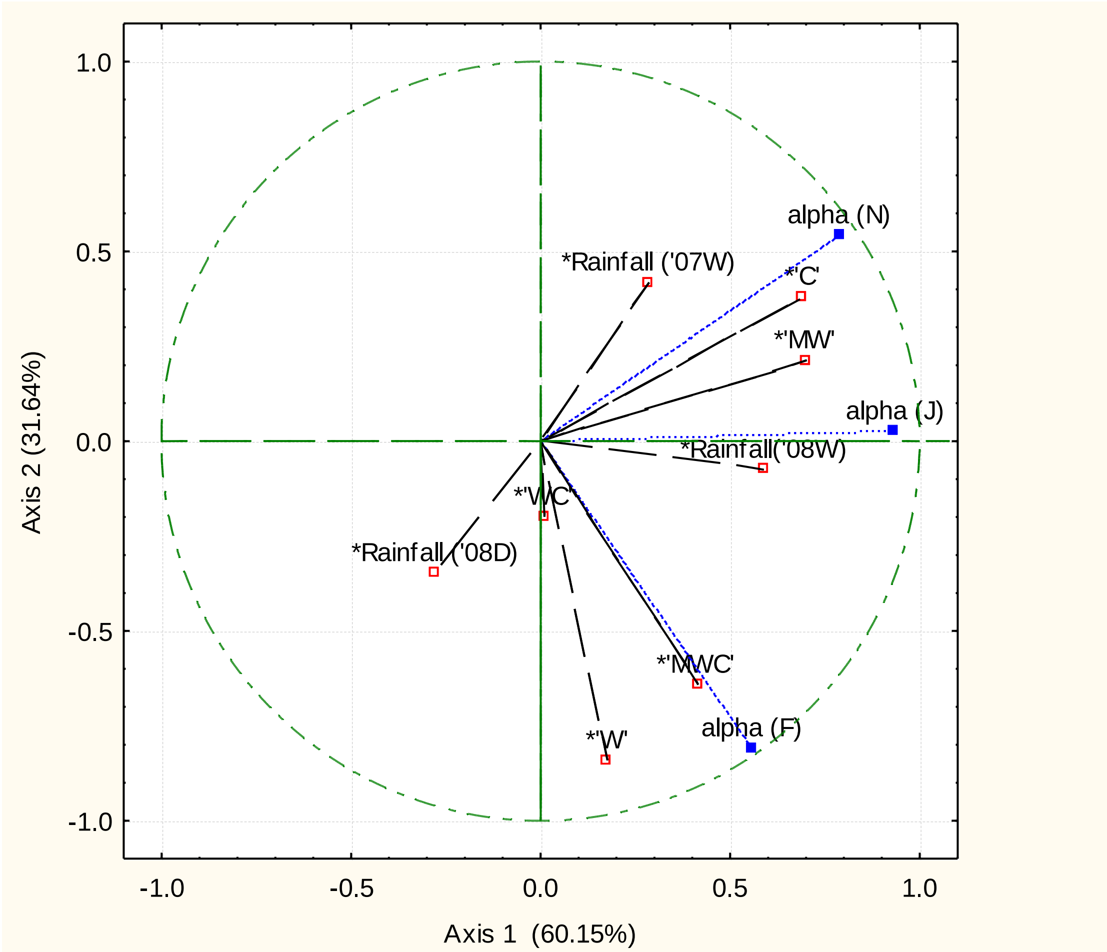

Figure 5. Ordination plot of the alpha diversity (plant species richness) to the grazing intensity and rainfall (determinant variables). The data were obtained from three sites; south, central and north at study site. The symbols; N, F and J represent November, February and June months in which alpha diversity measurements were taken during the (07W), (08D) and (08W) seasons respectively. The grazing herbivores (W, MW, C, WC, and MWC) and seasons are indicated by dashed lines, while the alpha diversity is represented by dotted lines. 07W, 08D and 09 indicate 2007 wet, 2008 dry and 2008 wet seasons.

The results indicated that 60 % variance of plant species richness was due to herbivore type, while the second axis indicated that 31 % of the variance of plant species richness was influenced by rainfall (the season). Therefore, 91 % variation in species richness at the study site was due to herbivore type grazing and rainfall, while 9 % was accounted for by other environmental factors apart from herbivore type and amount of rainfall. The ordination using the two axes suggests that the herbivore type and amount of rainfall were the main factors determining the plant species richness; however, herbivore type had more impact on the plant species richness than the amount of rainfall.

Beta diversity (plant species turn-over)

There were strong positive correlations between November and June beta diversity (β-N and β-J) and the amount of rainfall in the 2007 wet season, grazing by cattle and cattle grazing with wild herbivores (C, WC and MWC). There was also a strong correlation between February beta diversity (β-F) and the amount of rainfall in the 2008 wet season. However, there were negative correlations between β-N and β-J and the amount of rainfall in the 2008 dry season (Fig. 6).

The first axis of the PCA ordination indicates that 93.6 % of the variance on the species turn-over was due to the influence of herbivore type, while the second axis indicates that 4.9 % of the variance of species turn-over was due to the influence of amount of rainfall. Therefore, 98.5 % species turn-over at the study site was associated with herbivore type, while 1.5 % of the species turn-over was influenced by other environmental factors such as soil, apart from herbivore type and rainfall. The ordination using the two axes suggests that herbivore type had more influence on the plant species diversity than other environmental factors.

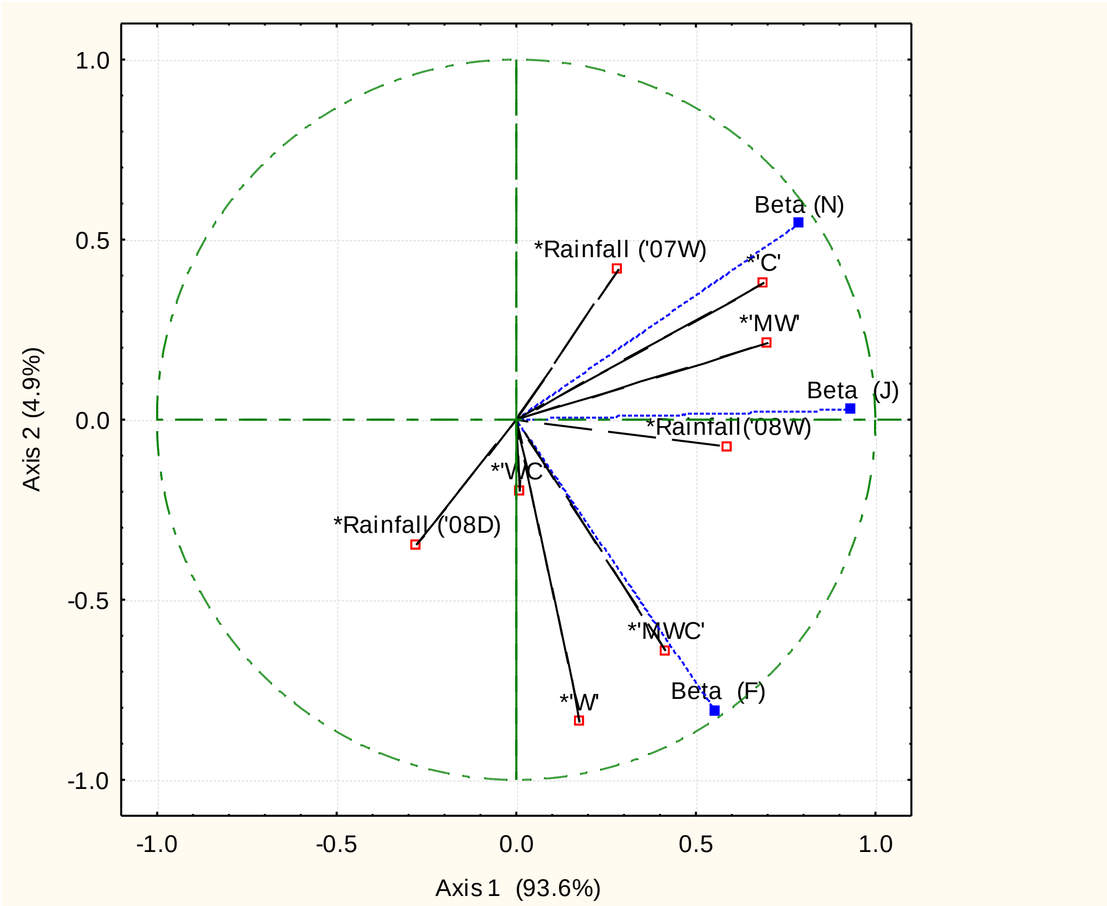

Figure 6. Ordination plot of the beta diversity (species-turn over) to the grazing intensity and rainfall (environmental variables). N, F and J represent November, February and June months in which measurements were taken during the (07W), (08D) and (08W) seasons.

Table 2: Percent frequencies of less dominant grass species in the exclosures in 2007 wet and 2008 dry seasons

Grass species	% frequencies in exclosures in wet season						% frequencies in exclosures in dry season					
	O	W	MW	C	WC	MWC	O	W	MW	C	WC	MWC
Brachiaria eruciformis	3	4	3	4	5	11	5	7	9	17	28	35
Sporobolus festivus	2	1	1	2	3	3	0	0	0	3	4	5
Eragrostis tenuifolia	1	1	1	1	5	13	0	1	3	1	5	13
Aristida congesta	2	1	1	1	1	3	1	1	1	2	3	3
Dinebra retroflexa	1	1	1	0	0	0	2	18	24	22	26	57
Microchloa kunthii	9	4	5	3	2	3	8	6	6	4	4	3
Digitaria milanjiana	7	4	5	2	2	2	7	5	4	3	2	3

Table 3: Percent frequencies of forb species in the exclosures in 2007 wet and 2008 dry seasons

Grass species	% frequencies in exclosures in wet season						% frequencies in exclosures in dry season					
	O	W	MW	C	WC	MWC	O	W	MW	C	WC	MWC
Aeva lanata	52	38	24	20	18	10	50	32	19	18	15	10
Aspilia pluriseta	42	35	34	36	27	24	32	32	28	28	26	24
Pseudognaphalium declinatum	39	33	24	15	13	11	34	33	25	14	12	13
Monechma debile	52	32	28	26	18	5	47	26	18	16	20	10
Dyschoriste radicans	42	34	32	31	30	28	50	31	32	25	30	25
Commelina erecta	10	10	11	14	20	26	12	14	16	20	38	52

Discussion

The effects of grazing by wildlife and cattle on plant species composition in the pasture

The large (>6 %) decrease in the proportions of tall coarse grass species (*Pennisetum stramineum* and *P. mezianum*) in the rangeland due to grazing by wildlife compared to ungrazed exclosures was probably because of selective feeding patterns of wildlife. Mega-herbivores (elephants and buffaloes) are bulk feeders and the intensive grazing to fill the gut may have led to low proportions of the tall grasses in the pasture and ultimately affect the composition of plant community in the pasture. The preference for tall grasses by wild non-ruminants (zebra and elephants) was because of longer period of microbial fermentation due to enlarged hind-gut (caecum and large intestine) that can increase nutrient absorption from low quality fibrous grass forage (Langer 1988).

Conversely, the small decrease in the proportions of *P. stramineum* and *P. mezianum* (<7 %) due to grazing by cattle compared to ungrazed exclosures in the wet season was probably because of avoidance of coarse grasses and preference for palatable grasses in the pasture. This view is supported by high (9 % and 11 %) decrease in the proportions of *Brachiaria lachnantha* and *Themeda triandra* due to grazing by cattle in the dry season. The intensive grazing by cattle resulted in low proportions of *Brachiaria lachnantha* and *Themeda triandra* in the exclosures grazed by cattle. At high stocking rates cattle bite rates increase but step rates decrease during grazing thus concentration of grazing by cattle on localized grazing points with palatable grass plant species (Odadi *et al*. 2009). The high (>10 %) decrease in the proportions of *P. mezianum* due to grazing by cattle during the dry season indicate that during periods of forage scarcity, cattle feed on the available forage irrespective of the poor quality.

The intensive grazing by cattle resulting in a decrease in proportions of the dominant grasses reduced the competitive ability of dominant grasses benefiting the suppressed less dominant grasses; *Aristida congesta, Brachiaria eruciformis, Cyperus elatus, Dinebra retroflexa*, *Eragrostis tenuifolia* and *Sporobolus festivus* and hence increase in frequencies of less dominant grasses in the pasture (Tables 2).

The less dominant grass species were buffered against heavy grazing by cattle and wild herbivores by growing among tall *Brachiaria lachnantha*, *Pennisetum stramenium*, *Pennisetum* *mezianum* and *Themeda triandra* grasses. With the suppression of dominant grass species, reducing competitive ability for light, soil moisture and nutrients leads to increase in less dominant grasses in the pasture. This is an example of "associated resistance" in which some plants such as *Brachiaria eruciformis* take advantage of growing under dominant plants of higher or lower palatability (Milchunas & Noy-Meir 2002; Hamback & Beckerman 2003). Intensive grazing by cattle increases the grazing-resistant species in the pasture (Adler & Morales 1999; Fowler 2002; Hickman & Hartnett 2002).

High frequencies, thus abundance of less palatable grass species such as *Aristida congesta*, *Dinebra retroflexa* and *Sporobolus festivus* was likely due to the invasion of these grass species as a result of over-utilization of the dominant grasses by intensive grazing. Increaser II grasses rapidly grow in overgrazed and degradaded rangelands (van Oudtshoon 1999) unlike Increaser I grasses increase in under-utilized rangeland. However, the decrease in the abundance of forbs in the exclosures (Table 3) grazed by cattle may be explained by non-selective and intensive grazing by cattle, consuming less palatable forbs in the pasture. The forbs that are more abundant may not necessarily be the most preferred, however, herbivores may consume less preferred plants during periods of food scarcity (Owen-Smith 1993).

The effects of grazing by wildlife and cattle on the plant species richness and species diversity in a pasture

Grazing by wild herbivores and cattle had an effect on the plant species richness and turn-over in the exclosures. Although there was a larger increase in species richness and species turn-over in the wet than in the dry season, grazing by herbivores had greater impact on species richness and diversity than the influence of the season. Grazing intensity determined the response of the species richness and diversity in the exclosures with an increase of species richness and turn-over with an increase in stocking rates (Figs. 5 and 6), that is, there were high increases in alpha and beta diversity as a result of grazing by cattle. High species diversity was probably due to competitive exclusion of tall grasses, forbs, shrubs alleviating light limitations that enhanced recruitment of more grasses and forbs in the pasture. Feeding by cattle reduces the impact of the dominant plant species (Milchunas & Lauenroth 1993). The high species turn-over in the exclosures grazed by cattle is in agreement with Connell's (1978) intermediate disturbance hypothesis which predicts that at moderate levels of disturbance, there is maximum species diversity and at low levels of disturbance (low grazing intensity) competitively superior species exclude subordinate species, whereas intense grazing disturbance reduces the competitively superior species allowing the establishment of suppressed species in the pasture, thus increasing species richness.

Low stocking rates of wild herbivores at the study site (0.004 – 0.05 livestock units per hectare) and selective grazing contributed to low plant species diversity in the exclosures grazed by wild herbivores compared to 0.12 – 0.16 livestock units per hectare (which is effective stocking rate of the site). Selective feeding on forbs and browse by small wild herbivores may have less effect on the canopy cover of the dominant grassess and hence light limitation, inhibiting germination and establishment of new plants. Furthermore, frequent movement by wild herbivores in and out of the exclosures (personal observation) may also have contributed to low plant species richness and species turn-over in the exclosures grazed only by wildlife. This is because with frequent movement, wildlife spent less time feeding on forage in an area, leading to low forage consumption thus less effect on dominant forb species. The negative correlations between grazing herbivores (wildlife and cattle) and species richness and turn-over during the dry season was because of absence of annual plants, only perennial plants were present, thus low plant species diversity. However, a decrease in plant species turn-over would also occur in situations of large numbers of wild herbivores in small reserves with a possibility of resource limitation (Mwasi 2002). High plant species richness and turn-over in the wet season implied a response of plants to increase of soil moisture. Plant species richness will be at maximum at moderate environmental resource (e.g. precipitation, nutrients) levels (Pausas & Austin 2001). For instance, the moderate rainfall results in less leaching of nutrients, thus nutrients are readily available for growth of an array of plant species in the pasture. The wet season enhanced the germination and growth of perennial and annual grasses and forbs that lead to high diversity in grazed exclosures. Grazing modifies some patterns of plant distribution through the influence of selective grazing on plant demographic processes, e.g. seed production, dispersal, seedling establishment, plant mortality or biotic interaction (McNaughton 1985; Senft *et al.* 1987; Wallis De Vries & Daleboudt 1994; Fuls 1992; Basigato & Bertiller 1997; Adler & Lauenroth 2000). Selective defoliation and trampling may also lead to a change in vegetation pattern and species composition (Sternberg *et al.* 2000). On communal grazing lands with large numbers of livestock and wildlife grazing together, the effects of heavy grazing on the proportions of herbaceous forage plants may be greater than the results obtained in the exclosures. This is because heavy grazing may lead to decline in plant species and increase in bare soil (Landsberg *et al.* 2002). The findings of this study show that grazing by wildlife cause less changes in the proportions of the dominant grass species compared to effect of cattle grazing which does not support the hypothesis that grazing by wildlife decreases dominant grasses in plant commmuty in semi-arid lands.

Conclusion

The changes in the proportions of dominant grasses, alpha and beta diversity in exclosures due to grazing by wildlife and cattle demonstrates the impact of grazing on forage resources on rangelands on which livestock and wildlife simultaneously utilize forage resources. A change in botanical composition, particularly from perennial to annual plants due to grazing by cattle could be detrimental on communal grazing lands leading to degradation of rangelands. It is apparent that the presence of wildlife on communal grazing lands will have an effect on the availability of forage plants for cattle and consequently reduce cattle performance. Therefore, monitoring of livestock stocking rates on communal grazing lands is important for sustainable use of rangeland resources. The appropriate livestock stocking rates will minimize effects of competition for forage between livestock and wildlife and enhance high quality livestock products to meet the needs of the pastoralists whose survival depends entirely on livestock.

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CHAPTER THREE

Effects of grazing by cattle and wild herbivores on forage utilization in Semi-arid lands, Kenya

Abstract

Livestock owners living in arid and semi-arid lands in Kenya believe that large wild herbivores compete with their livestock for grazing resources and pastoral communities that live adjacent to Tsavo and Amboseli National Parks and Maasai Mara and Samburu Game Reserves have chased away and sometimes killed wild herbivores on communal grazing lands particularly during the dry season when there is scarcity of pasture. Studies that have been conducted to determine competition for use of forage resources between wildlife and livestock have focused mainly on the comparative resource use, with emphasis on dietary overlap in the plant species consumed between wild herbivores and livestock. However, no study has been conducted to relate level of forage utilization by wildlife in the pasture, particularly the dominant perennial grass species to residual biomass of herbaceous layer. This study investigated the effect of forage utilization by wild herbivores and cattle on the residual biomass of the dominant grasses, which are the principal forage-producing plants in semi-arid lands in Kenya. It was conducted in the exclosures at Mpala Research Centre. Observations were made on the plant species consumed by zebra, oryx, hartebeest, Grant's gazelle and cattle during feeding. The level of utilization of dominant grasses was assessed by measurement of stubble heights of dominant grasses at twenty sampling points in ungrazed and grazed exclosures. The difference in mean stubble height in ungrazed and grazed exclosures was converted to percentage utilization by herbivores, whereas residual biomass was evaluated by clipping and weighing the herbage of grass species in $1m^2$ quadrats in grazed exclosures. The data were collected during the wet and dry seasons to determine seasonal variation in percentage utilization and residual biomass of the dominant grasses. Grasses provided over 50 % of the herbivore diet in the wet and dry seasons and there was a very highly significant ($p<0.0001$) overlap in plant species consumed between cattle and

wild herbivores. The results show low utilization (<13 %) with high residual biomass (>900kgs/ha) of dominant grasses in exclosures grazed by wildlife, whereas high utilization (>40 %) with less than 250 kgs/ha residual biomass in exclosures grazed by cattle. Although there was high overlap in plants consumed between cattle and wild herbivores, high residual biomass of dominant grasses in exclosures grazed by wildlife implied a conservative use of forage resources by wildlife.

Introduction

Increase in wildlife population on communal grazing lands is perceived to compete for forage with livestock and is of great concern to ranchers and pastoralists (Georgiadis *et al.* 2003). Pastoralists and wildlife have co-existed in African rangelands for many hundreds of years (Boyd *et al.* 2006). However, there is an increase in human-wildlife conflicts on communal grazing lands adjacent to protected areas (Boyd *et al.* 2006), increasing competition for forage resources between livestock and wildlife (Reid 2006), with resultant effect on perennial grasses, reducing the available forage in the pasture (Lamprey & Hussein 1981). Competitive interactions are expected especially when grazing behaviour of wild herbivores and livestock are similar (Van Wieren 1996; Prins & Olff 1998), particularly between cattle and zebra with similar diets (Casebeer and Koss 1970; Voeten 1999) Moreover, in many areas in east Africa, the effects of domestic livestock, especially cattle, on grass species have been considered to override those of wildlife (Frost *et al.* 1986). However, these effects have not been quantified, more so on the semi-arid communal grazing lands inhabited by nomadic pastoralists and their livestock (Keya 1998).

Forage utilization

Utilization or offtake can be defined as the amount of forage consumed or removed by herbivores. It is expressed as a percentage of the biomass available to the animal (Keya 1998). The level of forage utilization and residual forage biomass are linked to stocking rates and carrying capacity of the rangelands (Keya 1998). Heavy stocking rates reduce palatable plants and increase unpalatable forage plants and reduce forage intake by grazing herbivores Lyons *et al.* 2002). However, differential selection of forage plants among grazing herbivores may lead to complementary use of plant resources (Nolan *et al.* 1999).Utilization studies are important in grazing allotment and make short-term adjustment in stocking rates (Smith *et al.* 2005) (Fig.7 f).

The influence of herbivore species and body size on forage utilization

The amount of forage intake by herbivores is determined by the density of forage on offer (Allden & Whittaker 1970, Stobbs 1973 a,b, Short 1986) and in ruminants digestibility of the food determines the passage rate of the food in the gut and hence the amount of forage intake. Intake of nutrients and energy can be expressed as the product of the amount of ingested food (Illius *et al.* 1999), the body size of herbivore which influences the minimum quantity and quality of forage necessary for survival and the feeding niche selected (Heikkila & Harkonen, 1996). Variation in diet and habitat selectivity across ungulate species, as a result of the variation in body size and dietary tolerance (du Toit & Owen-Smith 1989), contributes to the high heterogeneity of savannah landscapes (du Toit 2003). The small antelope, for example, require high quality (low fibre) food to satisfy their relatively high metabolic rates and this could explain the differences in the diets of various African ungulates (Bell 1970; Jarman 1974). The body size determines the amount of forage required to refill the digestive tract after the partial digestion and passage of previous meals (Illius & Gordon 1991; 1992) (Fig. 7 b).

The influence of botanical composition, quantity and quality on forage utilization

Two major sward structure components, height and bulk density, affect the ease with which forage can be harvested by grazing animals which influences the amount of forage intake (Silva & Pedreira 1996). The composition of plant species consumed by grazing animals varies depending on the amount of forage available in the pasture (Arnold 1960; Hardison *et al.* 1954). The differences exist because grazing animals prefer certain plants and plant parts over others (Theurer *et al.* 1976). Herbivores grazing on rangeland utilize a diversity of plant species in varying quantity and quality which in turn affect diet selection and consequently the amount of forage intake (Maryland 1999; Launchbaugh *et al.* 2001). Forage quality influences intake hence level of utilization of forage plants. Forage quality is influenced by forage species, maturity at time of consumption, soil fertility and environment (climate) (Cherney & Hall 2005).

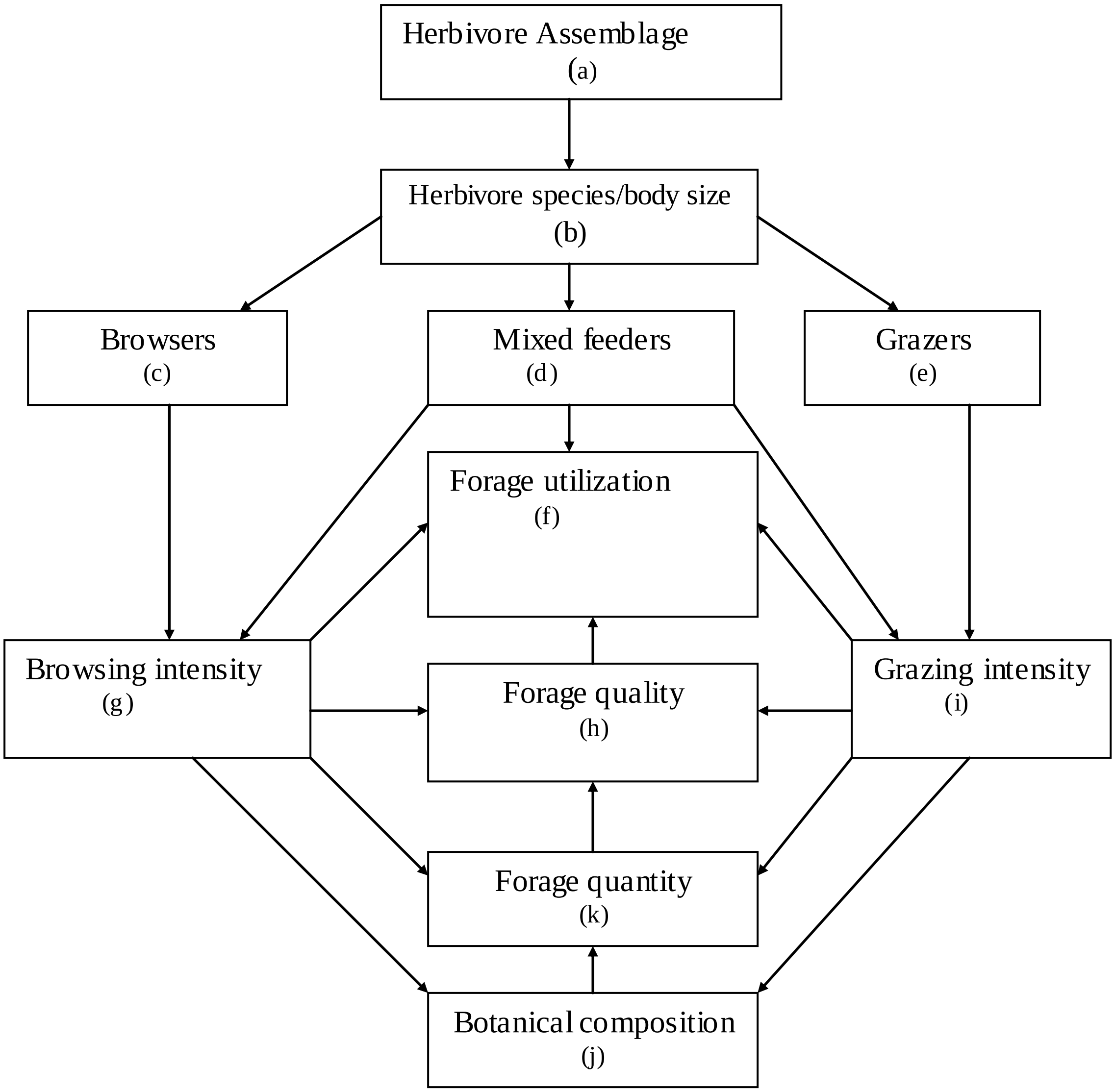

Figure 7: Factors that influence forage utilization by herbivores. The arrows show the direction of the influence.

Nutritional quality of forage plants is also affected by plant part, lignin content and secondary compounds (Lyons *et al*. 1989). Plant tissues with high crude proteins, lipids and starch are often preferred by grazing animals (McNaughton 1983; Vicari & Bazely 1993). Forage quality also influences energy and nutrient absoption (Van Soest 1982). Since preference by animals is positively correlated with plant quality (Marten 1978; Provenza 1995), herbivores generally prefer plant parts with highest nutrient concentrations and will compete for and increase intake of high quality forage during grazing (Launchbaugh *et al.* 1990). The quantity and quality of forage eaten not only determine the production of an animal species and reflect its behaviour and habitat (Milne 1991), but also provide reliable information on the value of those plants in addressing the nutritional needs of the individual (Minson 1990) (Fig. 7 h, j and k).

The influence of grazing and browsing intensity on forage utilization

Stocking density affects the quantity and mineralization of soil nutrient (Brookshire *et al.* 2002). Generally, forage production reduces as grazing intensity increases (Milchunas & Lauenroth 1993). Intensive grazing cause decline in ‘decreaser’ plants (most productive and palatable forage species) but increase under light stocking density (Smoliak 1974). As the stocking density increases, the level of forage utilization increases due to competition, resulting in a reduction in palatable and an increase in unpalatable plants (Redfearn & Bidwell 2008; Vendramini & Sollenberg 2007) (Fig.7 c, d, e, g and i).

It was hypothesized that wild herbivores have a high effect on the level of utilization and residual biomass of dominant grass species in semi-arid lands. Moreover, in many areas in east Africa, the effects of domestic livestock, especially cattle, on grass species have been considered to override those of wildlife (Frost *et al.* 1986). However, these effects have not been quantified, more so on the semi-arid communal grazing lands inhabited by nomadic pastoralists and their livestock (Keya 1998). Therefore, this study determined the level of forage utilization to evaluate the relationship between wild herbivores and cattle over use of forage resources in semi-arid lands in Kenya. The goal was to examine level of consumption of the dominant grass species by measuring the stubble heights in grazed exclosures to establish the impact of the level of utilization of dominant grasses by wild herbivores and cattle on the residual biomass of the grass species. The knowledge gained is to understand competitive and facilitative livestock-wildlife interactions on Kenyan rangelands. Residual biomass shows habitat condition and how well vegetation resources are maintained (Holechek & Galt 2000).

Material and methods

Experimental animals

Large wild herbivores selected for grazing observation included: zebra, Grant's gazelle, hartebeest and oryx. These wild herbivores were selected because of their abundance at the study site and also their feeding habits; grazers (zebra and oryx) and mixed feeders (Grant's gazelle and hartebeest). Although present, buffalo were not selected because of risk of attack during grazing observations. Cattle represented the domestic animals.

The plants consumed by herbivores were observed, identified and recorded during grazing and browsing in the exclosures. This method has been frequently used on wild (Lamprey 1963; Leuthold 1970; Croze 1974), tamed (Field 1968; Le Resche & Davis 1972), and domestic animals (Allden & Whittaker 1970). On each observation day, plants eaten by cattle, zebra, hartebeest, oryx, and Grant's gazelle were observed, identified and recorded. Observations on cattle were made from as close as 4 m, whereas the grazing wild herbivores were observed at a distance of 25 – 30 m using a pair of binoculars so that the wild grazers were not disturbed and put to flight. The feeding locations were identified using trees, bush or any physical object nearby. Immediately the animals moved to another grazing point, the observer moved to the previous grazing point, identified and recorded the plants eaten, by looking at freshly removed stems, shoots or leaves. The observations on wild herbivores were done in the morning and evening and cattle were observed during grazing in the exclosures, 08.00 – 12.00. Ten observations were made on each experimental type of animal within the exclosure on ten different days in each season. Total number of grass species, forbs, shrubs and trees eaten by each herbivore in the wet and the dry seasons was recorded and percentage frequency of each species in the wet and dry seasons calculated as follows:

$$\text{Frequency} = \frac{\text{Number of observations of particular plant species eaten}}{\text{Total number of observations}} \times 100$$

Utilization measurements of dominant grasses in the pasture

Stubble heights of the dominant grass species (*Pennisetum stramineum*, *Pennisetum mezianum*, *Brachiaria lachnantha*, *Themeda triandra*, *Lintonia nutans* and *Bothriochloa insculpta*) were measured during the wet and dry seasons. Stubble heights of each grass species were measured at twenty sampling points along five 100 m transect lines in the exclosures. At each sampling point, a 1 m^2 quadrat was laid out and heights of 10 to 15 grass plants of the same species inside the quadrat were measured (from base to the tip of the plant) by use of a 1 m rule. Ten to 15 plants were measured due to variability in heights of grazed plants. The stubble height measurements on each of the dominant grass species were taken in grazed and ungrazed exclosures in the south, central and the northern sites of the study area and the mean of stubble height of each dominant grass species for grazed and ungrazed exclosures calculated. The assumption was that growth rates of plants were the same in grazed and ungrazed plants. The percentage utilization of each grass species consumed by wild herbivores and cattle or cattle grazing together with wildlife was determined by the following formula:

$$\%\ \text{utilization} = \frac{\text{Mean height in ungrazed} - \text{mean stubble height in grazed exclosures}}{\text{Mean stubble height in ungrazed exclosures}} \times 100$$

The determination of residual biomass of each dominant grass was by clipping herbage of the dominant grass in the 1 m^2 quadrats at twenty sampling points along the 100 m transect lines in the grazed exclosures during the wet and dry seasons. The clipping was done to ground level and the material was oven-dried at 65°C to determine weight of dry matter. The mean dry weight of each grass species per 1 m^2 quadrat was computed and was used to calculate residual biomass (kgs/ha) in exclosures grazed by wildlife, cattle and cattle together with wildlife. The residual grass heights and biomasses were used to assess the effect of level of utilization on palatable and unpalatable dominant grasses by wildlife and cattle in semi-arid lands. A general linear regression model was also used to determine the effect of grazing by cattle with wild herbivores on the level of utilization of the dominant grasses in the exclosures.

Logarithmic transformation of the percentage utilization of the dominant grasses

The percentage utilization of each of the six dominant grasses: *Brachiaria lachnantha*, *Pennisetum stramenium*, *Pennisetum mezianum*, *Themeda triandra*, *Lintonia nutans* and *Bothriochloa insculpta* in the twenty sampling points in the exclosures grazed by large wildlife (W), large and mega-wildlife (MW) and cattle with wildlife (MWC) were converted into ratio of proportions (p) and the data transformed into log-values, i.e. $\hat{Y} = \log\left(\frac{p}{1-p}\right)$ (Dayton 1992). The log-odds values were used to evaluate how herbivore type and season affect level of utilization of the dominant grass species. The dominant grasses were selected since they formed over eighty percent of cover in the pasture and provided the bulk of forage to the herbivores. The effect of grazing by wildlife and cattle on utilization of grass species in the pasture was determined using a logistic regression model:

$\hat{Y} = w + m + c + y + s$

$\hat{Y}$ indicate log-odds of percentage utilization of grass species in the exclosures (dependent variable); "w" indicates the presence of large wildlife in the exclosures; "m" indicates the presence of mega-wildlife in the exclosures; "c" indicates the presence of cattle in the exclosures; "y" and "s" indicate the year and season when stubble height measurements were taken (independent variables). The transformation of the data into log-odds was to meet the assumptions for the linear models.

The presence or absence of large wildlife, mega-wildlife and cattle were coded as 1 and 0 respectively and the codes were used in the regression. Statistical Package for Social Sciences (SPSS) version 11.5 computer software was used in the regression analysis of independent variables (m + w + c) against the log-odds of the grasses in MWC exclosures (dependent variable). The inverse of the log (anti-log) of the coefficients of the estimates of the best fit regression line, i.e. $e^{(\hat{Y})}$ were used to calculate the proportions of grass species utilized by wildlife grazing alone and grazing by wildlife together with cattle.

Data analysis

Analysis of variance was done to show the significant differences in the relative frequencies of grass species, forbs, shrubs consumed among herbivores and also to determine significant differences in percentage utilization and residual forage biomass of dominant grass species in grazed exclosures during the wet and dry seasons. Logistic regression analysis was done using SPSS computer software whereby the log odds of percentage utilization of grass species by each herbivore (independent variables) were entered and the resultant coefficients in the regression model for each herbivore recorded. The anti-log of the coefficients (Beta) was used to determine the effect of the presence of each type of herbivore on the proportions of the stubble height of dominant grasses utilized in the pasture (exclosures).

The proportion of utilization of each grass species was determined using the following formula:

i.e. $x = \left(\dfrac{p}{1-p} \right)$; $x - xp = p$

$$x = p + xp$$
$$x = (p + xp)$$
$$\frac{x}{1 + x} = p$$

where: x is the anti-log of the log-odds ($\hat{Y}$) and p is the proportions of utilization of grass species in the grazed exclosures. Pearson bivariate correlation analysis was done to determine the overlap in consumption of grasses, forbs and shrubs between cattle and wild herbivores to assess the similarity in consumption of forage plants.

Results

Plant species consumed by herbivores

There were 80 herbaceous plant species at the study site of which 34 % were grasses and 66 % forbs; however grass formed over 80 % composition of cover of the pasture. Grasses were the most consumed herbaceous plants by all herbivores and the diet of each herbivore comprised over 40 % grass during the wet and dry seasons, whereas hartebeest and Grant's gazelle browsed on shrubs and trees, with high intake of browse during the dry season. Cattle diet comprised grasses and forbs, grass constituted over 83 % and forbs less than 15 % of the plants consumed during the wet season. Zebra and oryx consumed tall coarse grasses, which constituted over 87% of forage plants consumed and forbs contributed less than 13 % in the wet and dry seasons. However, in the dry season, cattle and oryx browsed on few shrubs in the pasture, with high intake of browse by cattle. Hartebeest and Grant's gazelle consumed grass species which constituted 71 % of the forage plants eaten and 23 % forbs and shrubs in the wet season, however in the dry season hartebeest and Grant's gazelle increased intake of browse and reduced amount of grass in the diet (Fig. 8).

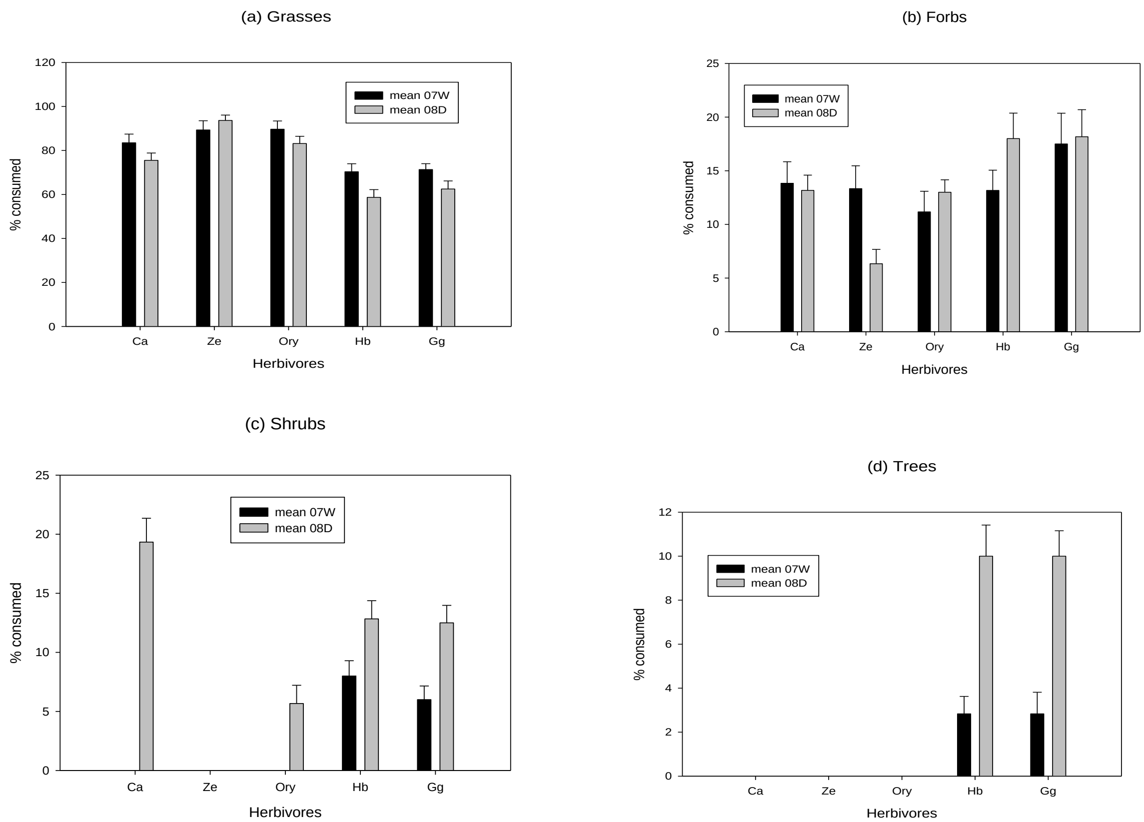

Figure 8. Seasonal variation in the frequencies of grasses, forbs, shrubs and trees in the diet of cattle (Ca), zebra (Ze), oryx (Ory), hartebeest (Hb) and Grant's gazelle (Gg). The error bars represent standard error (SE) at 95% CI.

The dominant grasses (*Themeda triandra*, *Brachiaria lachnantha*, *Pennisetum stramineum*, *Bothriochloa insculpta*, *Pennisetum mezianum* and *Lintonia nutans*) were consumed by all herbivores during the wet season (Table 2). However, *Themeda triandra* and *Brachiaria lachnantha* were the most consumed grasses by the herbivores during the wet and dry seasons, whereas *Pennisetum mezianum* was the least eaten grass species by cattle, hartebeest and Grant's gazelle during the dry season. *Rhynchosia nyasica*, *Indigorefa schimperi*, *Rhinacanthus ndorensis* and *Hibiscus flavifolius* were the most consumed forbs by cattle, oryx, hartebeest and Grant's gazelle in the wet and dry seasons, whereas *Searsia natalensis, Cadaba farinosa* and *Lycium shawii* were browsed by hartebeest and Grant's gazelle in the wet and dry seasons. *Searsia natalensis* and *Cadaba farinosa* were highly consumed by cattle, but less consumed by oryx during the dry season. *Pseudognaphaliun declinatum* was consumed only by zebra in the wet and dry seasons, whereas *Commelina erecta* and *Crotolaria brevidens* were only eaten by herbivores during the wet season.

The overlap in consumption of grass species, forbs and shrubs between cattle and wild herbivores varied from the wet to dry season (Table 3). There was high correlation (overlap) of grass species consumption between cattle and zebra, oryx, hartebeest and Grant's gazelle during the wet and dry seasons and high overlap of consumption of forbs and shrubs between cattle and small wild ungulates (hartebeest and Grant's gazelle) in the wet season. There was also a very high overlap in grass species consumed between cattle and zebra during the wet and dry seasons, and very high overlap between cattle and oryx, hartebeest and Grant's gazelle in the wet and dry seasons. Similarly, there was a very high overlap in the consumption of forbs and shrubs between cattle and hartebeest and Grant's gazelle, whereas high overlap between cattle and oryx, but no significant overlap between cattle and zebra during the wet season. However, there was no significant overlap in the consumption of forbs and shrubs between cattle and zebra, oryx, hartebeest and Grant's gazelle during the dry season which may be due to forage selection, with cattle consuming mainly grass species and wildlife feeding on forbs and shrubs.

Table 4 : The relative frequencies of plant species consumed by cattle and wild herbivores

Plant species	% frequencies of plants consumed Wet season						% frequencies of plants consumed Dry season					
	Cat	Zeb	Ory	Hb	G.gaz	Mean	Cat	Zeb	Ory	Hb	G.gaz	Mean
Grasses												
T. triandra	16	12	15	14	10	13.4	19	16	14	11	12	14.4
B. lachnantha	10	12	12	14	10	11.6	14	16	10	11	12	12.6
P. stramenium	10	16	6	5	7	8.8	8	18	12	4	8	10.0
B. insculpta	10	4	12	5	7	7.6	10	10	8	6	6	8.0
P. mezianum	8	16	6	3	5	7.6	4	14	6	2	4	6.0
L. nutans	6	6	9	6	7	6.0	10	4	6	4	4	5.6
M. kunthii	6	4	4	6	5	5.2	2	4	8	4	4	4.4
D. milanjiana	4	4	6	5	2	4.2	2	4	2	4	4	3.2
Chl. Virgata	2	4	4	5	5	4.0	-	2	6	4	4	3.2
C. ciliaris	4	2	6	3	3	3.6	2	2	6	-	2	2.2
E. tenuifolia	4	2	4	3	3	3.2	-	-	2	2	2	1.2
S. sphacelata	2	4	-	-	2	1.6	-	4	2	-	-	0.8
D. retroflexa	2	-	-	2	2	1.2	-	-	-	-	-	-
Sedge												
Cyperus elatus	2	2	4	2	3	2.6	-	-	-	-	-	-
Forbs/shrub												
R. nyasica	4	4	4	5	5	4.4	4	-	4	6	8	4.8
I. schimperi	4	2	2	2	5	3.0	4	-	4	7	4	4.2
R. ndorensis	2	2	2	3	3	2.4	2	-	2	2	4	2.4
H. flavifolius	2	-	2	2	3	1.4	4	-	2	2	2	2.8
C. brevidens	2	2	-	2	3	2.2	-	-	-	-	-	-
C. erecta	2	-	2	2	2	1.8	-	-	-	-	2	0.4
S. natalensis	-	-	-	2	2	1.2	8	-	2	2	2	2.4
C. farinose	-	-	-	3	2	0.6	10	-	2	4	6	4.0
L. shawii	-	-	-	3	2	0.4	-	-	2	7	4	2.2
A.drep	-	-	-	2	2	0.8	-	-	-	6	4	2.0
A. mellifera	-	-	-	-	-	-	-	-	-	4	2	1.2
P. declinetum	-	2	-	-	-	0.4	-	6	-	-	-	0.4

-Indicates that the plant species was not eaten by the herbivores during the period of observation.

Table 5: Pearson's bivariate correlation coefficient matrix (i.e. overlap of plant growth forms: Grasses; n = 14, df = 13, forbs and shrubs; n = 12, df = 11) derived from Table 16, % relative frequencies of grasses, forbs and shrubs in the diet of cattle and wild herbivores during the wet and dry seasons.

Herbivore species	Wet season Cattle		Dry season Cattle	
	Grasses	Forbs / shrubs	Grasses	Forbs / shrubs
Zebra	0.724**	0.495	0.772**	0.090
	P<0.003	0.102	P<0.002	0.780
Oryx	0.863**	0.693*	0.810**	0.130
	P<0.0001	P<0.013	P<0.0001	0.687
Hartebeest	0.778**	0.866**	0.871**	0.174
	P<0.0001	P<0.0001	P<0.0001	0.589
Grant's gazelle	0.870**	0.871**	0.893**	0.438
	P<0.0001	P<0.0001	P<0.0001	0.154

** Correlation is significant at the .01 level (2-tailed)
* Correlation is significant at the .05 level (2-tailed)

Regression analysis

The logistic regression model (Table 6) shows estimates of the proportions of the dominant grasses utilized by large wild herbivores (w), mega-wild herbivores (+m) and cattle (+c) grazing in the exclosures. In the 2007 season 12 – 14 %, 8 % and 15 – 21 % more of *Brachiaria lachnantha, P. stramineum* and *P. mezianum* were utilized by large wildlife and mega-wildlife, whereas 34 %, 27 % and 22 % more were utilized by cattle compared to exclosures grazed by large wildlife. In the 2008 dry season, 13 – 15 %, 17 – 20 % and 13 – 15 % more of *Brachiaria lachnantha, P. stramineum* and *P. mezianum* were utilized by large wildlife and mega-wildlife, whereas 23 – 25 % more were utilized by cattle compared to exclosures not grazed by large herbivores. However, in the 2008 dry season, 62 %, 56 % and 55 % more of *Themeda triandra, Lintonia nutans* and *Bothriochloa insculpta* were utlilized by cattle, whereas only 11 – 20 % more were utilized by large wildlife and mega-wildlife compared to exclosures not grazed by large herbivores. In the 2008 wet season, 12 – 16 % more of *Brachiaria lachnantha, P. stramineum* and *P. mezianum* were utilized by large wildlife and mega-wildlife, whereas 19 %, 23 % and 21 % more were utilized by cattle compared to exclosures not grazed by large herbivores. 55 %, 44 % and 43 % more of *Themeda triandra, Lintonia nutans* and *Bothriochloa insculpta* were utilized by cattle compared exclosures not grazed by large wild herbivores in the 2008 wet season. Conversely, only 11 – 16 %, 14 – 20 % and 12 – 19 % more of *Themeda triandra, Lintonia nutans* and *Bothriochloa insculpta* were utilized by large wildlife and mega-wild herbivores compared to pasture not grazed in the 2008 wet season. The results indicate that grazing by cattle at moderate stocking rates had more effect on palatable dominant grass species than grazing by large wildlife and mega-wildlife with low stocking rates at the study site.

Table 6: Estimates of the proportions of the dominant grasses utilized by large, mega-wildlife and cattle in the exclosures. L= lower limit; U=upper limit; CI= confidence interval: calculated by 2 x SE); SE=standard error and β= utilization coefficients; and the reference is the ungrazed exclosure (constant).

Season/grass species/ herbivore type 2007 wet season	Coefficient (β)	SE	95 % CI Bl (L)	Bl (U)	% estimates of proportions utilized by herbivores	Df	F	T	Sign	R^2
Brachiaria lachnantha										
Constant	-2.920	0.265	-3.450	-2.390	5	19	9.274	-1.830	0.086	.735
W	-1.433	0.235	-1.903	-0.963	19			-2.730	0.0001	
+ m	-1.560	0.157	-1.874	-1.246	17			-3.198	0.0001	
+ c	-0.446	0.264	-0.874	-0.016	39			-4.187	0.0001	
Pennisetum stramum			Ps (L)	Ps (U)						
Constant	-3.052	0.393	-3.838	-2.266	5	19	40.952	-1.552	0.140	.963
W	-1.914	0.412	-2.738	-1.050	13			-9.006	0.0001	
+ m	-1.878	0.395	-2.668	-1.088	13			-7.896	0.0001	
+ c	-0.720	0.288	-1.296	-0.144	32			-10.622	0.0001	
Pennisetum mezianum			Pm (L)	Pm (U)						
Constant	-2.804	0.428	-3.660	-1.948	6	19	19.745	-0.161	0.463	.787
W	-1.351	0.246	-1.843	-0.859	21			-4.660	0.0001	
+ m	-1.008	0.340	-1.629	-0.324	27			-3.480	0.003	
+ c	-0.900	0.176	-1.252	-0.548	28			-2.749	0.014	
Themeda triandra			Tt (L)	Tt (U)-						
constant	-2.972	0.368	-3.708	-2.346	5	19	17.307	-0.562	0.582	.747
W	-1.485	0.418	-2.321	-0.649	19			-4.315	0.0001	
+ m	-1.206	0.349	-1.904	-0.506	23			-3.003	0.0001	
+ c	-0.371	0.446	-0.473	-0.269	41			-6.810	0.0001	

Lintonia nutans			Ln (L)	Ln (U)						
Constant	-2.180	0.277	-2.734	-1.626	10	19	36.541	-0.963	0.074	.873
W	-0.905	0.230	-1.365	-0.445	28			-5.258	0.0001	
+ m	-0.837	0.143	-1.123	-0.551	30			-4.958	0.0001	
+ c	-0.469	0.301	-0.571	-0.367	39			-7.266	0.0001	
Bothriochloa insculpta			Bi (L)	Bi (U)						
Constant	-3.065	0.353	-3.771	-2.249	5	19	51.210	-1.244	0.093	.939
W	-1.820	0.413	-2.646	-0.994	14			-9.315	0.0001	
+ m	-1.759	0.320	-2.399	-1.119	15			-7.081	0.0001	
+ c	-0.582	0.330	-0.842	-0.322	25			-11.51	0.0001	
2008 dry season										
Brachiaria lachnantha			Bl (L)	Bl (U)						
Constant	-2.790	0.329	-3.448	-2.136	6	19	70.11	-0.586	0.216	.940
W	-1.351	0.165	-1.681	-1.025	21			-8.291	0.0001	
+ m	-1.480	0.236	-1.952	-1.008	19			-6.566	0.0001	
+ c	-0.823	0.133	-1.089	-0.557	31			-10.60	0.0001	
									Ps (U)	
Pennisetum stramineum			Ps (L)	Ps (U)						
Constant	-3.005	0.480	-3.965	-2.411	5	19	115.85	-1.518	0.089	.965
W	-1.109	0.300	-1.709	-0.509	25			-8.524	0.0001	
+ m	-1.274	0.428	-2,130	-0.418	22			-12.27	0.0001	
+ c	-0.925	0.470	-1.165	-0.685	28			-16.16	0.0001	
							Pm (U)			

Pennisetum mezianum			Pm (L)	Pm (U)						
Constant	-2.631	0.489	-3.609	-1.653	7	19	8.387	-0.836	0.416	.611
W	-1.250	0.327	-1.904	-0.596	22			-2.360	0.003	
+ m	-1.416	0.265	-1.946	-0.886	20			-2.944	0.0001	
+ c	-0.803	0.133	-0.969	-0.637	31			-3.511	0.0001	
Themeda triandra			Tt (L)	Tt (U)						
Constant	-2.599	0.430	-3.491	-1.707	7	19	59.749	-1.098	0.231	.923
W	-1.236	0.254	-1.744	-0.728	23			-9.947	0.0001	
+ m	-1.490	0.305	-2.100	-0.880	18			-10.50	0.0001	
+ c	0.476	0.362	-0.562	-0.390	62			-13.26	0.0001	
Lintonia nutans			Ln (L)	Ln (U)						
Constant	-1.968	0.442	-2.852	-1.084	12	19	86.319	-1.872	0.201	.946
W	-0.773	0.096	-0.969	-0.577	32			-11.17	0.0001	
+ m	-0.800	0.142	-1.084	-0.516	31			-9.256	0.0001	
+ c	0.259	0.318	0.154	0.364	56			-16.65	0.0001	
Bothriochloa insculpta			Bi (L)	Bi (U)						
Constant	-2.460	0.430	-3.320	-1.600	8	19	39.521	-1.180	0.121	.740
W	-1.215	0.254	-1.723	-0.707	22			-4.615	0.0001	
+ m	-1.378	0.255	-1.888	-0.868	20			-3.358	0.0001	
+ c	0.294	0.322	0.230	0.358	55			-6.195	0.0001	

2008 wet season

Brachiaria lachnantha			Bl (L)	Bl (U)						
Constant	-2.901	0.292	-3.485	-2.317	5	19	42.439	-1.909	0.074	.888
W	-1.520	0.310	-2.140	-0.900	18			-5.203	0.0001	
+ m	-1.318	0.309	-1.936	-0.700	21			-4.894	0.0001	
+ c	-1.176	0.352	-1.480	-0.872	24			-7.742	0.0001	
										Ps (U)
Pennisetum stramineum			Ps (L)	Ps (U)						
Constant	-3.116	0.335	-3.786	-2.446	4	19	57.815	-1.196	0.249	.912
W	-1.638	0.279	-2.196	-1.080	16			-9.132	0.0001	
+ m	-1.490	0.324	-2.138	-0.842	20			-6.408	0.0001	
+ c	-0..854	0.115	-1.084	-0.624	30			-4.821	0.0001	
Pennisetum mezianum			Pm (L)	Pm (U)						
Constant	-2.875	0.403	-3.681	-2.069	5	19	9.274	-1.830	0.86	.635
W	-1.628	0.322	-2.272	-0.984	16			-4.730	0.0001	
+ m	-1.462	0.328	-2.118	-0.686	19			-3.198	0.0001	
+ c	-1.042	0.164	-1.370	-0.714	26			-2.187	0.0001	
Themeda triandra			Tt (L)	Tt (U)						
Constant	-2.655	0.420	-3.495	-2.687	7	19	30.162	-1.863	0.081	.793
W	-1.390	0.284	-1.958	-0.822	20			-2.362	0.002	
+ m	-1.542	0.335	-2.212	-0.872	18			-7.664	0.004	
+ c	0.193	0.016	0.162	0.224	55			-9.376	0.0001	

Lintonia nutans	Ln (L)		Ln (U)							
Constant	-2.781	0.394	-3.569	-1.993	6	19	44.937	-1.913	0.85	.894
W	-0.803	0.163	-1.129	-0.479	31			-6.021	0.0001	
+ m	-0.950	0.235	-1.420	-0.480	28			-7.265	0.0001	
+ c	-0.185	0.031	-0.246	-0.124	44			-10.161	0.0001	
Bothriochloa insculpta	Bi (L)		Bi (U)							
Constant	-2.595	0.352	-3.299	-1.891	7	19	19.745	-01.161	0.263	.787
W	-0.684	0.109	-0.902	-0.466	33			-4.660	0.0001	
+ m	-0.820	0.186	-1.192	-0.448	31			-3.480	0.003	
+ c	-0.270	0.027	-0.323	-0.217	43			-5.769	0.0001	

w =The estimates of the proportions of dominant grasses utilized by large wildlife (zebra, oryx, hartebeest, Grant's gazelle); + m = Proportions of dominant grasses utilized by mega- wildlife (elephants and giraffes) and + c = Proportions of dominant grasses utilized by cattle.

Forage utilization and residual biomass

There was a high utilization of *Brachiaria lachnantha, Themeda triandra* and *Lintonia nutans* in exclosures grazed by cattle, with a small amount (<300kgs/ha) residual biomasses (Fig. 9 a, g, i and b, h, j). In contrast, there were low utilization of *Brachiaria lachnantha* and *Themeda triandra* (<13 %), with a large amount (>900kg/ha) residual grass biomass accumulation in exclosures grazed by wildlife during the wet and dry seasons. *Themeda triandra* and *Brachiaria lachnantha* were the most utilized grasses in exclosures grazed by cattle, with over 50 % utilization and less than 250 kg/ha residual biomass accumulation, implying *Themeda triandra* and *Brachiaria lachnantha* were the most preferred grasses in exclosures grazed by cattle. *Pennisetum mezianum* was least utilized in the exclosures grazed by cattle. There were very highly significant differences in percentage utilization and residual forage biomass among grazed exclosures during the wet and dry seasons.

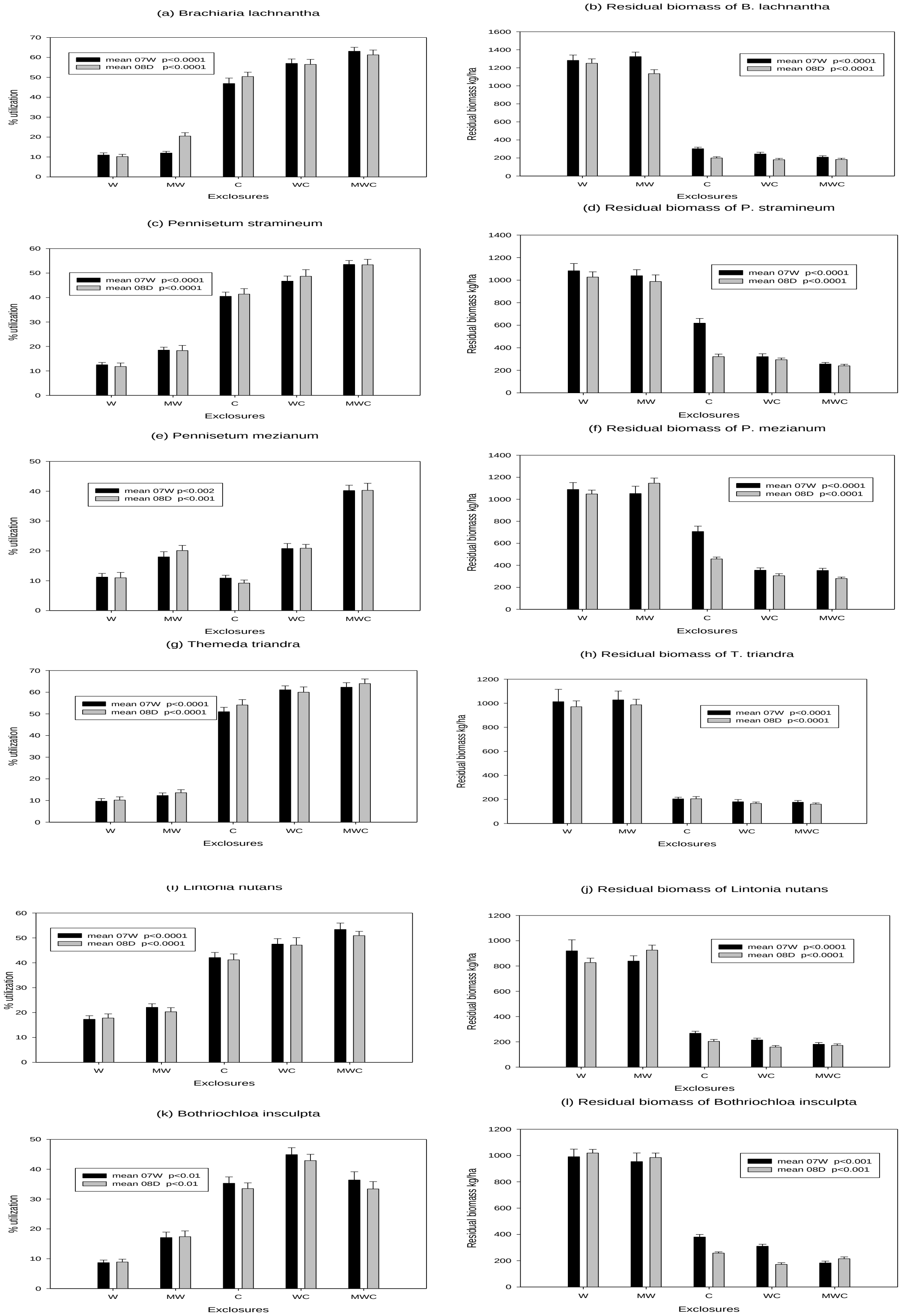

Figure 9. Seasonal variation in percent utilization and residual biomass of dominant grasses: *Brachiaria lachnantha*, *Pennisetum stramineum*, *Pennisetum mezianum*, *Themeda triandra*, *Lintonia nutans* and *Bothriochloa insculpta* in the exclosures during the 2007 wet and 2008 dry seasons.

Discussion

Preference for forage plants influenced the level of utilization of forage plants by grazing herbivores. High consumption of grasses by the grazers (cattle, zebra and oryx) and high consumption of forbs and shrubs by mixed feeders (hartebeest and Grant's gazelle) was influenced by quality of forage and nutritional requirements of herbivores. Selective feeding on palatable grasses, forbs, shrubs and trees by wild herbivores contributed to less than 27 % utilization resulting in high grass biomass in the exclosures grazed by wild herbivores. Removal of between 0 – 30 % of grass height is considered light use (Holechek and Galt 2000). Light and moderate defoliation increase growth rates and high accumulation of residual forage biomass in the exclosures grazed by large wildlife.

Co-existence of grazing herbivores might be realized through differences in body size, leading to differential preference for forage height and quality (Illius and Gordon 1987, 1992). For instance, zebra have longer retention times of food in the digestive system to absorb more energy in dry forage (Wilmshurst, 2000; Codron 2006). However, small wild ungulates such as Grant's gazelle and Dik dik with small digestive systems reduces digestibility of coarse grass vegetation (Peters 1983; Owen-Smith 1988; Clauss & Hummel 2005; Gagnon 2000; Fritz & Duncan 1994; Wilmshurst 2000; Jarma 1974). The leaves of trees are easily digested providing high energy requirements, unlike in coarse grasses with high content of cellulose that reduces digestibility of the cell wall (Demment & van Soest 1985). Furthermore, wild herbivores alter their habitat use and diet seasonally, so that competition may be minimized during times of scarcity (Owen-Smith 1989). Selective feeding of forage plants by wild herbivores in exclosures is in agreement with the niche concept (Hutchison 1958), which postulated that a niche is a "hypervolume" in a multidimensional ecological space for species reproduction and survival and the coexistence of different animal species since they are not using the same niche. Grazing on tall grasses by zebra in the exclosures (as indicated in Chapter 5) is also in agreement with results by Arsenault and Owen-Smith (2008) at Hluhluwe-imfolozi Park, Kwazulu-Natal, which indicated that zebra consumed grass taller than 20 cm in the pasture.

Conversely, intensive utilization of *Themeda triandra*, *Lintonia nutans*, and *Bothriochloa insculpta* by cattle, especially during the dry season with more than 62 % utilization, resulted in decrease in residual biomass in exclosures grazed by cattle. Based on grazing intensity guidelines (Holechek and Galt 2000), over 50 % utilization of *Themeda triandra*, *Lintonia nutans* and *Bothriochloa insculpta*, by cattle in the dry season (Table 6) implies heavy grazing. The grazing intensity guidelines indicate that removal of 51 – 60 % grass height is heavy grazing. Heavy grazing of *Themeda triandra* (>53 % utilization), for instance, had an effect on the regenerative capacity of the grazed grass as heavy grazing removes the growing points of tall grasses (Lyons & Hanselka 2003), reducing growth potential of plants and thus there is a decline in residual forage biomass. Defoliation treatments that remove more than 30 % of the annual biomass production reduce the residual biomass of forage plants (Clay 1995). The decrease in residual biomass of the dominant grasses due to grazing by cattle in the exclosures was in agreement with observations made by Tiffen *et al*. (1994), which indicated a low proportion utilized and high biomass of grasses in lightly grazed and high proportions of grass species utilized and low biomass on heavily grazed portions of rangeland. Domestic livestock (cattle, sheep and goats) show a high degree of utilization of palatable grasses and rejection of unpalatable grasses (Pisani *et al*. 2000), thus decline biomass of palatable and high proportions of unpalatable grasses in grazed areas (Llorens 1995: Distel & Boo 1996). Palatable grass species are higher in protein and lower in structural carbohydrates than the unpalatable species (Moretto & Distel 1997; Cerqueira *et al*. 2004).

Although *Pennisetum mezianum* was a dominant grass species in pastures at the study site, its low consumption (21 – 24 % level of utilization) by cattle was probably due to low palatability. *Pennisetum mezianum* has a high carbon: nitrogen ratio (44.1:5.01) when mature (Dougall & Glover 1964), thus reducing its palatability since a high carbon: nitrogen ratio and high lignin content reduces palatability in range grasses and hence it is avoided by grazing animals (Moretto & Distel 1997; Moretto *et al.* 2001). The increase in utilization with subsequent decrease in residual forage biomass of palatable plant species by cattle may exacerbate competition between cattle and large wild herbivores for nutritous forage plants in semi-arid lands. Rapid decline in forage biomass due to intensive forage utilization by cattle may augment competition for forage resource between cattle and wildlife on communal grazing lands. Competition may arise when there is low forage biomass and when the difference in body sizes is too small (e.g. between cattle and zebra), thus resource competition is expected to prevail over facilitation (Prins & Olff 1998).

The findings of this study demonstrate that grazing by wildlife consumes small amounts of forage resulting in high residual biomass, whereas high forage utilization by cattle results in rapid decline in residual biomass. Although a moderate stocking density of cattle was used in the exclosures grazed by cattle, the results show high utilization of palatable dominant grass species with low residual biomass (<300kg/ha). The findings imply that the effect of continuous grazing by large herds of livestock and wildlife on communal grazing lands with a stocking density of 4 L.U/ha is likely to be greater than the effects exhibited in the exclosures. The intensive grazing by cattle on palatable dominant grasses with consequent decline in forage biomass may lead to displacement of wild herbivore grazers such as zebra and wildebeest with similar body size as was observed by Young *et al.* (2005), a strong suppression of zebra population in plots grazed by cattle because wild herbivores with similar body size as cattle consume large amounts of forage, thus a high effect on available forage biomass. Therefore, the results do not provide evidence that that wildlife grazing affect residual biomass of the dominant grasses.

Conclusion

The level of utilization and consequent residual biomass of dominant grass species in a pasture is influenced by palatability of the grass species. The decline in residual forage biomass, particularly of palatable grasses is likely to result in competition between livestock and wild herbivores on communal grazing lands because each herbivore tends to increase intake of the available forage resource in the pasture. The findings of this study provide evidence that the observed decline in forage by pastoral communities on communal grazing lands in Kenya is as a result of high grazing intensity by livestock and not because of presence of wild herbivores. The pastoralists need to incorporate wildlife in livestock production systems instead of eradicating it as its presence may have a complementary effect on forage available for cattle.

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CHAPTER FOUR

Plant biomass response to grazing intensity by wild herbivores and cattle in semi-arid lands, Kenya

Abstract

Controversy over grazing resources has gained momentum in semi-arid lands in Kenya with ranchers and pastoralists arguing that wild herbivores compete with livestock for forage on communal grazing lands resulting in a decrease in forage biomass. However, no study has been conducted to determine the amount of forage consumed by wild and domestic herbivores sharing forage resources on rangelands or communal grazing lands to ascertain the potential for competition between wildlife and livestock and thus an effect on forage biomass. This study investigated the impact of cattle and wildlife grazing on the forage biomass in semi-arid lands. The study was conducted in the Experimental Exclosures at Mpala, Laikipia District, Kenya. Forage biomass consumed by wildlife, cattle and cattle grazing together with wildlife in the exclosures was determined by measurements of forage height in $1m^2$ quadrats using a disc pasture meter. Measurements were taken at 100 sampling points along transect lines in each exclosure. The settling height of the disc pasture meter on forage in the quadrat was recorded and using a conversion table, the mean forage height in each exclosure was converted to forage mass per hectare. Forage mass in caged plots was also determined with a disc pasture meter. Forage biomass consumed by the herbivores in the grazed exclosures was calculated by subtracting the mean forage biomass in grazed exclosures from that in ungrazed exclosures. The increment in forage biomass over a three month interval in wet and dry seasons was determined in a number of the $1m^2$ plots in each plot (grazed and ungrazed). Some cages were clipped to 10 cm high to simulate moderate grazing and then enclosed with a rodent proof wire mesh to determine effects of grazing on regrowth. Forage mass was also measured at fifty randomly selected points in open grazed areas in the exclosures. The results showed that wildlife consumed less than 50 % of the forage biomass consumed by cattle, with a very highly significant ($p< 0.001$) difference in mean

forage biomass consumed between exclosures grazed by cattle and those grazed by wildlife. In contrast, there was high increment in forage biomass inside the caged plots in the exclosures grazed by cattle and little increment in ungrazed exclosures. These results indicate that grazing by wildlife does not reduce the amount of forage in the exclosures and thus grazing by wildlife has no effect on the availability of forage for livestock in semi-arid lands.

Introduction

Appropriate grazing is critical in semi-arid lands in order to reduce the effects of grazing on forage biomass and species composition (Briske *et al.* 2008), because grazing is assumed to affect forage production on rangelands (Briske *et al.* 2008). The impact of grazing on forage biomass is influenced by growth responses of plant species to grazing, with some plants increasing in biomass and productivity, other plants decreasing in biomass and productivity and some plants decreasing in biomass but increasing productivity (Reeves & Champion 2004). Overgrazing reduces forage production, reduces plant growth and affects the composition of grasses, shrubs and forbs that comprise the forage and browse for livestock and wildlife (Krausma *et al.* 2009).

Forage production

Forage production is influenced by biotic and abiotic factors that include precipitation, plant species composition and grazing herbivores (Hooper 2005; Hector 2005). Forage biomass is defined as the above-ground dry organic matter per unit area (e.g. gm^{-2}), and productivity is defined as the biomass production (primary production) per area per time unit (e.g. $gm^{-2}yr^{-1}$: Noy-Meir 1975; Newman 1993). Sustained forage production depends largely on the vigour and persistence of the perennial grasses, the principal forage-producing plants in grasslands (McCarty

& Price 1942) and accurate assessment of standing crop or plant biomass is essential for sustainable utilization of forage resources (Webb 1942; Benkobi *et al*. 2000) and for grassland or rangeland condition (‘t Mannetje 2000) (Fig. 10 q).

The influence of mammalian herbivory on plant forage production

Grazing by herbivores influences forage production (Cumming 1982; Crawley 1983; Seastedt 1985; Detling 1987; McNaughton *et al*. 1988; Sala 1988) and above-ground biomass of grasses (Ferraro & Oesterheld 2002). Depending on environmental conditions and morphological development, defoliation by herbivores impacts forage biomass and quality (Brueland *et al*. 2003). Forage production declines with increases in grazing frequency and intensity (Manske 1998) with resultant low plant biomass (Briske & Richard 1995; Manske 1998; Trlica 1999). Nevertheless, the growth response of forage plants to defoliation can be positive due to increase in tiller production (Ferraro & Oesterheld 2002) and thus African ecosystems support large quantities ofgrazing herbivores because of this positive response of forage to grazing (Fig. 10 a, b and h).

The influence of herbivore species, body size and grazing history on forage production

Forage biomass is influenced by the type and size of herbivore utilizing the forage plants in the pasture (Bell 1970; Jarman 1974). In ruminants, the amount of forage consumed depends on the quality of forage on offer (Briske *et al*. 2008). Bulk grazing by cattle frequently affects the below ground biomass of grasses (Hunting Technical Services 1977; Schwarz & Schultka 1995) reducing their regenerative and production potential. However, feeding on tall coarse grasses by non-ruminants (e.g. zebra) during the dry season enhances accessibility of short grass swards to smaller ungulates (Bell 1971; Beekman & Prins 1989). Grazing by zebras benefits cattle by eating fibrous, woody grasses exposing the more delectable, higher-protein grasses beneath (Tenenbaum 2014).

Although rangelands with a long history of grazing are characterized by short and intermediate-height grasses with low forage biomass (Milner 2002) browsing by elephants (non-ruminants) opens up dense shrubland stands and increases the abundance and forage production of the herbaceous layer (van Wijngaarden, 1985) (Fig. 10 b, d and s).

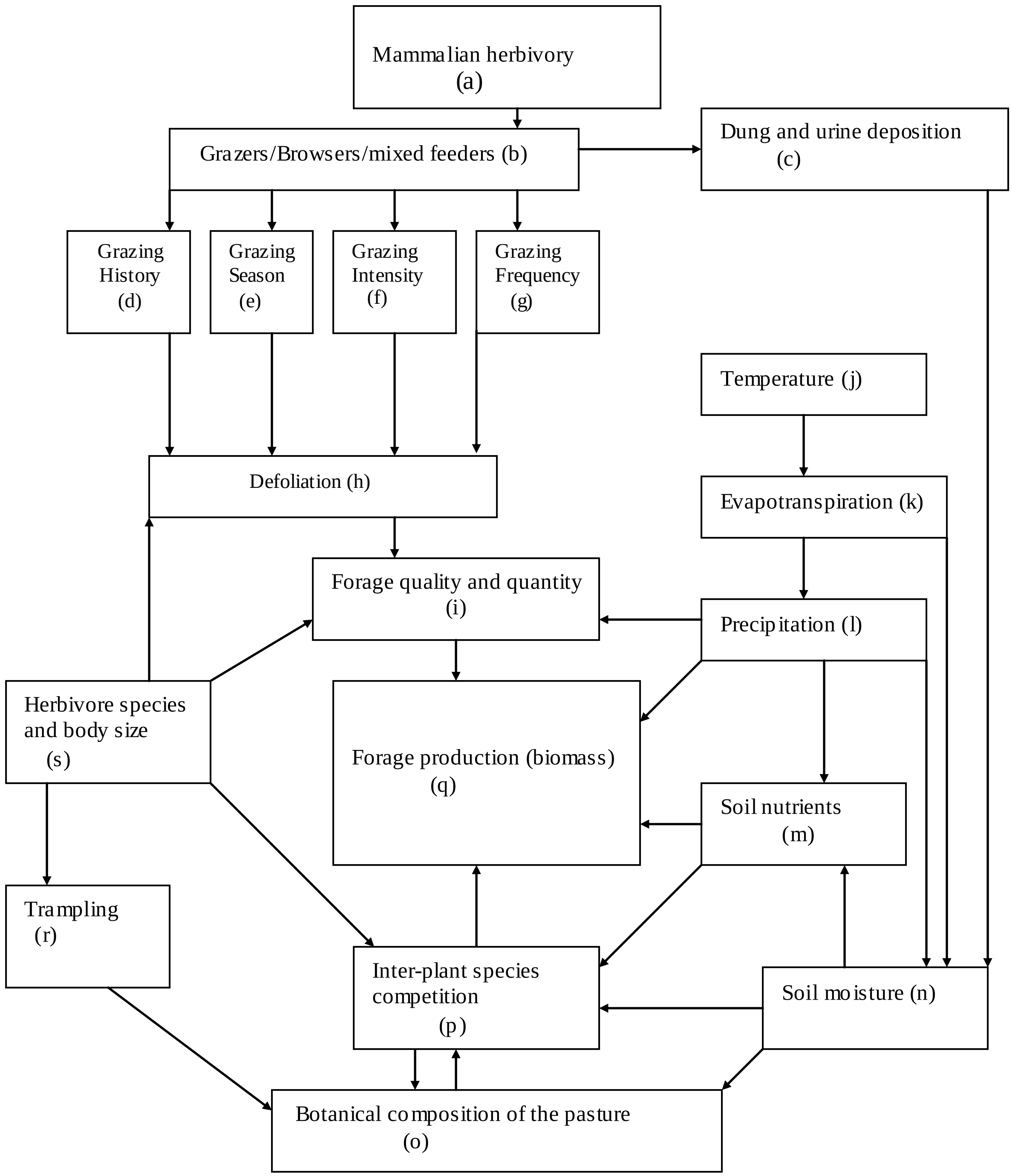

Figure 10: Factors that influence forage production. The arrows indicate the direction of influence.

The influence of season, intensity, frequency of grazing and forage quality on forage production

Time of grazing with respect to the phenological stage of the plants consumed has been proposed to be the most important external factor affecting post-herbivory compensatory growth and influencing forage biomass (Whitham *et al.* 1991; Danell *et al.* 1994). Low grazing pressure and selective feeding by wild herbivores results in high forage biomass (Tainton *et al.* 1996; Rook *et al.* 2004) (Fig. 10 e, f and g). Forage quality in range plants is also influenced by factors such as soil fertility, stage of growth and photosynthetic pathways (Hodges & Bidwell 1993; Redfearn 2008; Waller *et al.* 1985; Huston & Pinchal 2008). The most important constituents to describe forage quality have been digestible dry matter (energy), crude protein, and fibre contents which influence the intensity of grazing and the amount of forage intake by herbivores (Allden & Whittaker 1970, Stobbs 1973a, b; Short 1986; Sanderson & Wedin 1989; Mitchel *et al.* 2005) (Fig. 10 i).

The influence of precipitation, temperature, soil nutrients and trampling on forage production

In semi-arid environments, water usually is considered the limiting factor in biomass production (Herlocker 1999) and in rangelands with high precipitation results in high forage biomass (Mei *et al.* 2004). Rainfall in semi-arid lands is highly variable, erratic and unreliable in terms of amount, time and space, with a mean annual rainfall that ranges between 250 – 600 mm (Pratt & Gwynne 1977). Temperature is seldom limiting to plant growth in arid and semi-arid lands (Lind & Morrison 1974; Pratt & Gwynne 1977) and neither is there much variation in the temperature regime, either seasonally or annually. However, high temperature in semi-arid and arid lands results in high evapotranspiration levels (Pratt & Gwynne 1977), which reduces soil moisture available to plant growth in rangelands (Fig.10 j, k and l). The semi-arid areas of

Laikipia Plateau are composed of poorly drained clay soils (D'Hoore in Morgan 1973), which hold more water than sandy soils and tend to be more fertile, and when adequate moisture is available, produce more palatable and nutritious fodder (Walker 1993). Livestock and wildlife may increase soil fertility through dung and urine deposition, accelerating the nitrogen mineralization rate (Afzal & Adams 1992; Russelle 1992; McNaughton *et al.* 1997; Rotz *et al.* 2005) that increases nutrient availability especially in soils with low nutrients (Semmartin & Oesterheld 2001) (Fig. 10 m and n).

Trampling damages pastures by causing soil compaction, where air or water filled pore spaces are replaced by soil particles, which hinder air circulation in the soil, reducing plant growth and yield (Staff 2004; Chaichi *et al.* 2005). Nevertheless, trampling could have a positive impacts, e.g., loosening the soil surface for better water infiltration or compacting sandy soil so that root-soil contact is improved. Intensive grazing and trampling reduces plant species composition and cover, affecting nitrogen fixation and nutrient and water movement in the soil which impede root growth, plant growth and plant productivity (Staff 2004) (Fig. 10 r).

The effects of plant species composition and inter-plant species competition on forage production

Inter-specific plant competition reduces yield of plants growing together (Mynhardt *et al.* 1992, Nafziger 2006), thus inter-specific plant competition has an influence on plant growth since they compete for light, nutrients, water and space (Braun-Blanquet 1979). Plants which are not well adapted may be deprived of their light energy requirements by more competitive neighbours and therefore grow slower than they would in the absence of competition (Mynhardt *et al.* 1992) (Fig. 10 o and p).

It was hypothesized that grazing by wildlife result in the decrease in forage biomass in semi-arid lands in Kenya. Generally, it is assumed by ranchers and pastoralists that wild herbivores compete with livestock for forage on communal grazing lands affecting forage available for livestock (Georgiadis *et al.* 2003). However, no study has been conducted to assess the amount of forage consumed by wild and domestic herbivores sharing forage resources on rangelands or communal grazing lands to ascertain the potential for competition between wildlife and livestock and thus the effect on forage biomss.

Materials and methods

Sampling procedure/ herb layer biomass estimates

One hundred sampling points were marked along 10 transect lines in each of the ungrazed and grazed (O, W, MW, C, WC and MWC) exclosures and forage height was measured at 10 m intervals using a disc pasture meter (DPM) (Trollope & Trollope 1986, 2000) and the mean forage height was converted to mean forage mass in each exclosure. A disc pasture meter was used because of the reliable results that were obtained for measurements of forage production and fuel load in grasslands (Trollope & Trollope 1986, 2000; Zambatis *et al.* 2006). The height at which a disc pasture meter settles above the ground is dependent on the density of forage and a mean is required for accurate forage determination if the height of forage varies within an exclosure. The 100 sampling points were taken to reduce sampling error and thus increase the degree of accuracy of forage mass estimates. The sampling points were evenly distributed at ten metre intervals along ten transects, thus the mean forage heights and mean forage mass were representative of the forage biomass in the exclosures. The forage height measurements were taken at three month intervals, i.e. first week of November 2007, February 2008 and June 2008. The disc pasture meter was lowered onto the forage plants in each 1m^2 quadrat and the settling height recorded. The mean height per quadrat in each exclosure was calculated and converted to mean forage mass (Kg ha^{-1}) using a conversion table developed by Zambatis *et al.* (2006) on tall grasslands in a semi-arid environment with two calibration equations for the disc pasture heights of ≤26cm and ≥26cm. Those equations are;

Kg ha^{-1} $[31.7176\,(0.3218^{1/x})\,x^{0.2834}]^2$ ($r^2 = 0.951$; $P < 0.0005$)
and
Kg ha^{-1} $[17.3543\,(0.9893^{x})\,x^{0.5413}]^2$ ($r^2 = 0.882$; $P < 0.0005$), respectively,

where x is the mean height in cm of a site.

The mean forage mass (biomass) measurements were taken in the ungrazed and grazed exclosures at the beginning and end of three month intervals. The differences in forage height and hence forage mass at the beginning and end of three months intervals were the amount of forage consumed in the wet and the dry seasons:

i.e. $FWc = FW_b - FW_e$ (1)

where FWc is the forage mass consumed (i.e. the difference in forage mass at the beginning and end of the three month interval), FW_b is the forage mass at the beginning and FW_e is the forage mass at the end of the three month interval.

Measurement of increment in forage biomass in exclosures

A pair of $1m^3$ rodent proof movable cages were firmly placed at different points in each exclosure. Forage inside one of the pair of cages was clipped at 10 cm above the ground to simulate moderate grazing, whereas forage in the other caged plot was not clipped. Fifty 1 m^2 quadrats were also placed along transect lines in the exclosures. The clipped and unclipped forage height inside the caged plots and forage height in quadrats outside caged plots (open areas) in exclosures was measured by use of a disc pasture meter (DPM) and measurements were repeated after three months in the wet and the dry seasons. The mean forage height of clipped and unclipped in the caged plot and forage height in $1m^2$ quadrats in each exclosure was converted to forage mass using a conversion table by Zambatis *et al.* (2006). The difference in forage mass at the beginning and end of the three months interval (August and October 2007 wet season), (December and February 2008 dry season) and (April and June 2008), were the estimates of potential increment of forage biomass.

i.e. $Rfi = FWt_1 - FWt_0$ (2)

where Rfi is the increment in forage biomass in exclosures, FWt_1 is the forage mass in caged plots and in $1m^2$ of grazed plants in the exclosures at the end of the season (three months intervals), FWt_0 is the forage mass in caged plots and open grazed areas in the exclosures at the beginning of the season. Forage measurements in the pair of caged plots were taken at two different sampling points in the exclosures to estimate mean forage biomass increment in the exclosures. The difference in mean forage mass between unclipped and clipped caged plots and mean of forage mass in open areas grazed by herbivores were calculated to determine impact due to the grazing by herbivores (i.e. grazing by wildlife and cattle) on potential increase in forage biomass.

Data analysis

Means of forage weight in exclosures were computed using descriptive statistics whereas analysis of variance (ANOVA) was used to determine the significant differences in mean forage weight among the exclosures. The total forage biomass in each exclosure was determined by multiplying forage forage mass per hectare by the 4 hectares.

Results

The total forage biomass in ungrazed was higher in wet and dry seasons compared to grazed exclosures, whereas the forage biomass was more in the wet seasons than in the dry season. However, the total biomass in exclosures grazed by cattle was less compared to biomass in exclosures grazed by wild herbivores (Table 7). There was no significant ($p>0.05$) difference in forage biomass between ungrazed (O) and exclosures grazed by large wildlife (W) and large wildlife grazing with mega-wildlife (MW). However, there was a significant ($p<0.047$) difference in forage biomass between exclosures grazed by cattle alone (C) and (O), whereas a highly significant ($p<0.01$) difference between exclosures grazed by cattle with wildlife (WC and MWC) and O in the 2007 wet season. There was a highly significant ($p<0.024$) difference between W, MW and O, whereas a very highly significant ($p<0.001$) difference in forage biomass between C, WC, MWC and O.

Table 7. Total biomass (kilogrammes) in exclosures in wet and dry seasons

Exclosures	2007 wet season	2008 dry season	2008 wet season
O	24288	22848	23692
W	23240	18696	20072
MW	23416	17952	19752
C	23012	13788	16892
WC	22492	13940	15484
MWC	21544	13992	16172

Small amounts of forage were consumed in the ungrazed (O) and exclosures grazed by wildlife (W and MW) in the wet season and in the dry season compared to the total available forage biomass in the exclosures. Comparatively, large amounts of forage were consumed in the exclosures grazed by cattle (C, WC and MWC) in the wet season but less was consumed in the dry season (Fig. 12). There were very highly significant differences in forage biomass and amount of forage consumed by herbivores among the exclosures in the wet and dry seasons. There was a significant ($p<0.03$) difference in the amount of forage consumed in the exclosures grazed by mega-wildlife and large wildlife, whereas very significant ($p<0.005$) and ($p<0.0001$) differences in the amount of forage consumed between C, WC, MWC exclosures and W and MW.

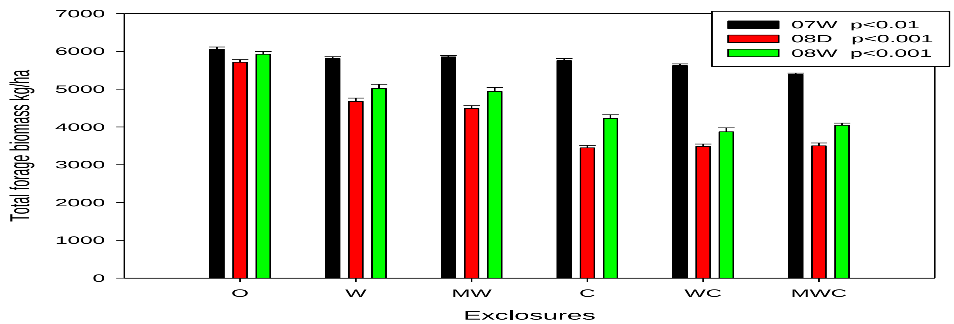

Figure 11: Variation in forage biomass (kgs/ha) in ungrazed and grazed exclosures in the 2007 wet, 2008 dry and 2008 wet seasons. W, MW, C, WC, and MWC represent W, MW, C, WC, and MWC represent the exclosures grazed by largr wildlife, large and mega-wildlife, cattle, cattle with large wildlife, cattle with large and mega-wildlife. 'M' is the mega-wild herbivores.

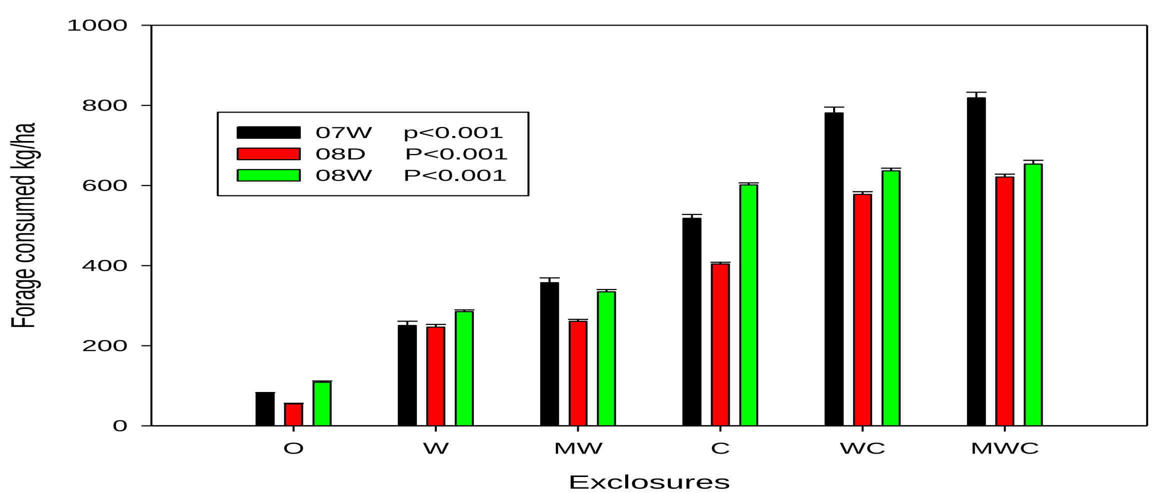

Figure 12: Variation in forage biomass (kgs/ha) consumed in ungrazed and grazed exclosures in the 2007 wet, 2008 dry and 2008 wet seasons.

Increment in forage biomass in exclosures

There were high increments in biomass in unclipped and caged, clipped and caged plots and open grazed areas (no clipping) in exclosures grazed by cattle (C, WC and MWC), with highest increment in unclipped and caged and clipped and caged plots in the C exclosure in the 2007 wet season and the lowest in the unclipped and caged plot in the ungrazed (O) exclosure in the wet and dry seasons. The high increment in the unclipped and caged, clipped and caged plots was an indication of increase in the number of tillers produced due to protection of plants from intensive grazing by cattle, whereas the small increment in forage biomass in unclipped and caged, clipped and caged plots and open grazed areas during the dry season was due to insufficient soil moisture for plant growth (Figs. 13, 14 and 15). There were large (>100 Kg ha^{-1}) differences in increment in forage biomass in unclipped and caged plots between grazed and ungrazed exclosures compared to small (<50 Kg ha^{-1}) differences in forage increment in the clipped and caged plots between grazed and ungrazed exclosures in the 2007 and 2008 wet seasons (Fig. 14 and 15).

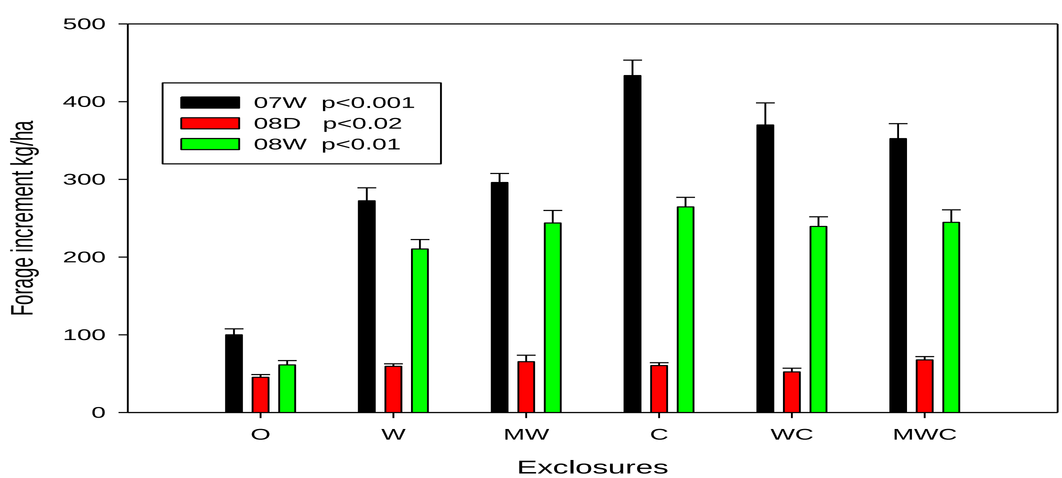

Figure 13. Seasonal variation in increment in forage biomass (Kg/ha/month) in unclipped and caged plots in the exclosures in the wet and dry seasons

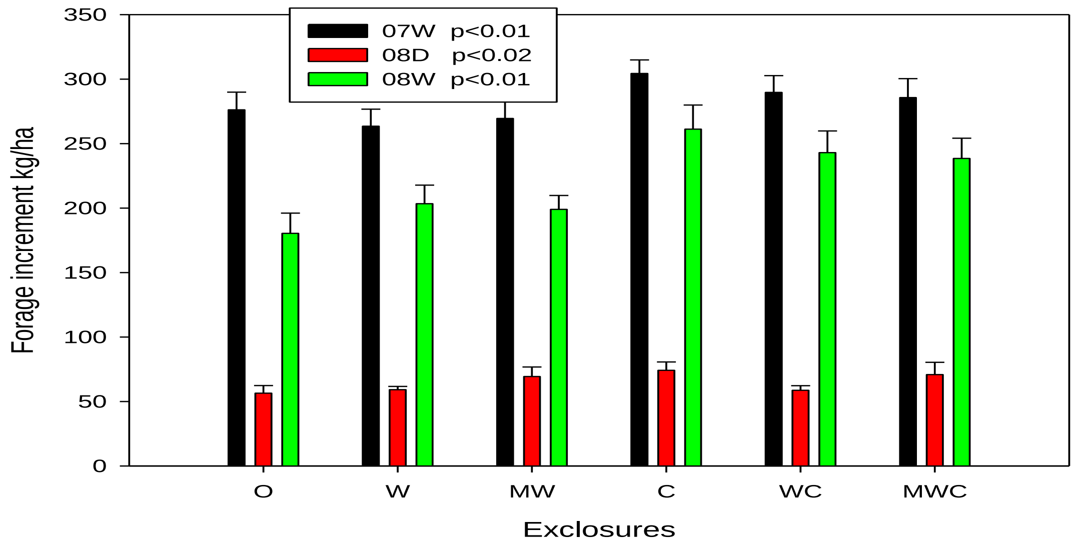

Figure 14. Seasonal variation in increment in forage mass (Kg/ha/month) in the clipped and caged plots in the exclosures (August 2007 – June 2008)

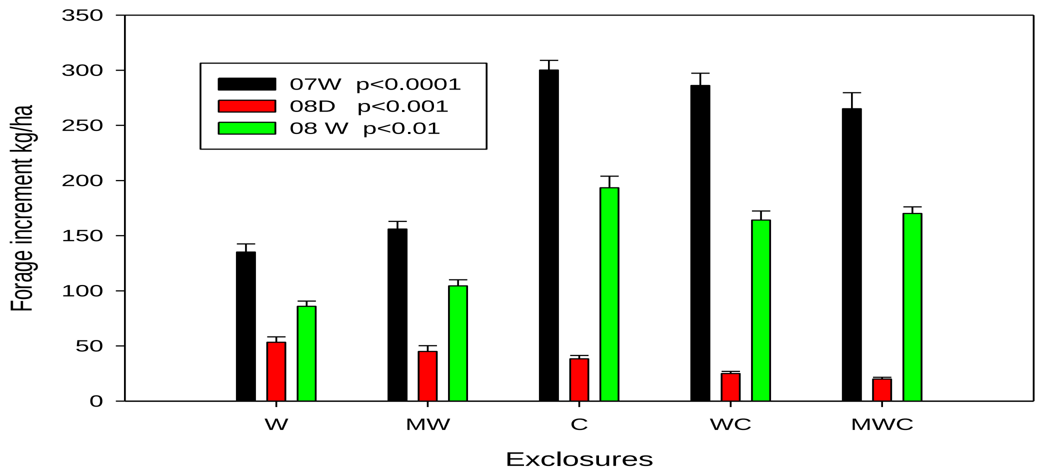

Figure 15. Seasonal variation in increment in forage biomass (Kg/ha/month) in open grazed areas (no clipping) in the exclosures in the wet and dry seasons

Effects of grazing on increment in forage biomass

There were large differences in increment in forage biomass between unclipped and caged plots and open grazed areas in the exclosures grazed by wild herbivores (W and MW) but slight differences in increment between unclipped and caged plots and open grazed areas in the exclosures grazed by cattle (C, WC and MWC) during the 2007 and 2008 wet seasons. Similarly, there were large differences in increment in forage biomass between clipped and caged plots and open grazed areas in the exclosures grazed by wild herbivores, whereas slight differences in increment in forage biomass between clipped and caged plots and open grazed areas in the exclosures grazed by cattle in the wet seasons (Figs. 16 and 17). However, there were small differences in increment in forage biomass between unclipped and caged, clipped and caged plots and open grazed areas in the W, MW, C, WC and MWC exclosure during the dry season (Fig. 18). The differences in increment in forage biomass between unclipped and caged, clipped and caged plots and open grazed areas in the exclosures demonstrate the response of forage biomass to grazing by wild herbivores and cattle grazing together with wildlife in semi-arid lands.

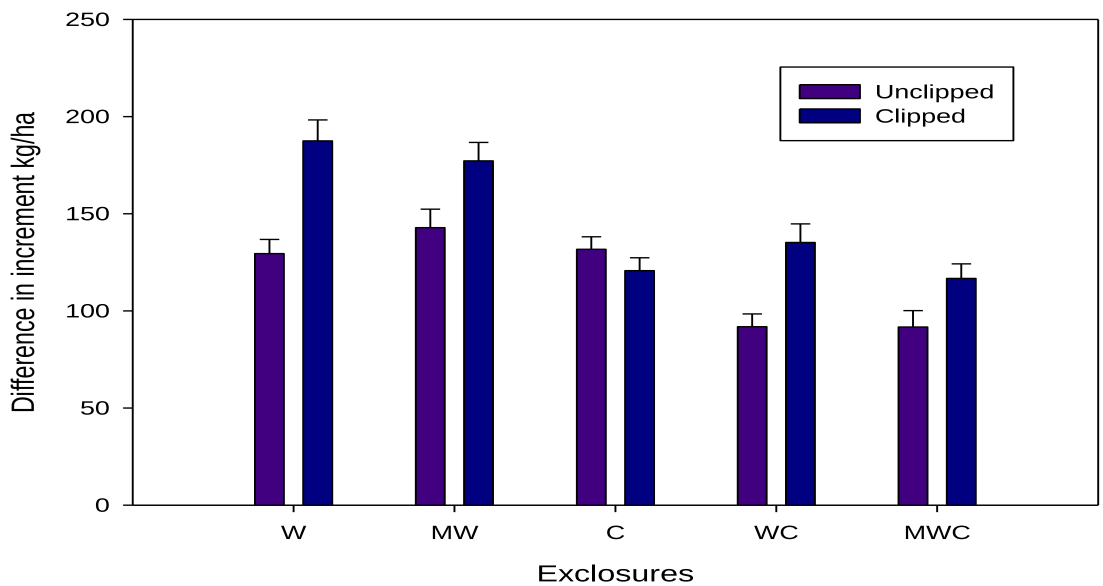

Figure 16. Difference in increment in forage biomass (Kg/ha/month) between caged plots with unclipped forage, caged plots with clipped forage and open grazed areas in the 2007 wet season (t_0 is at the beginning of August and t_1 at the end of October 2007).

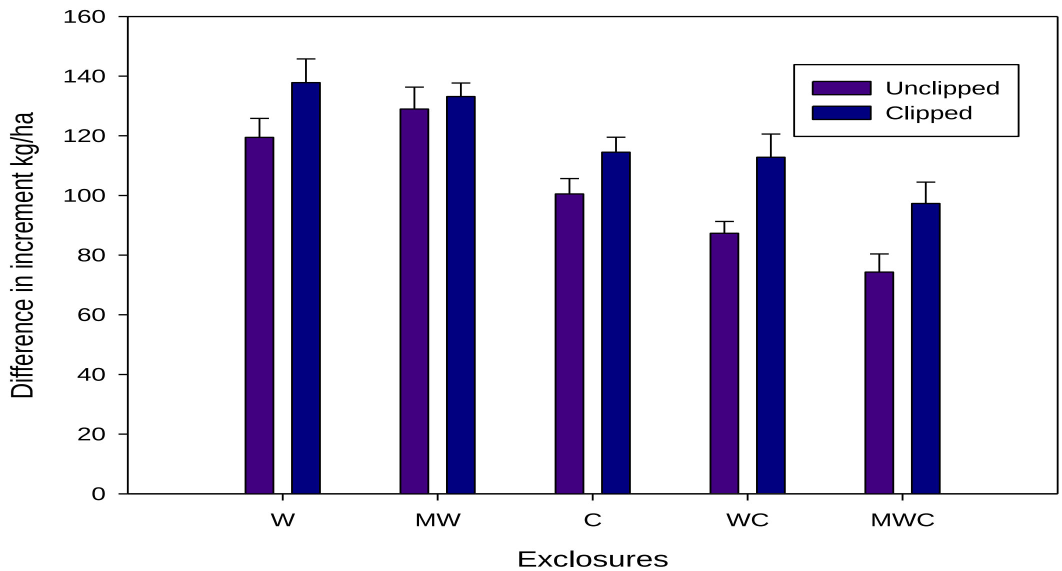

Figure 17. Difference in increment in forage biomass (Kg/ha/month) between caged plots with unclipped forage, caged plots with clipped forage and open grazed areas in the 2008 wet season (t_0 is at the beginning of April and t_1 is at the end of June 2008)

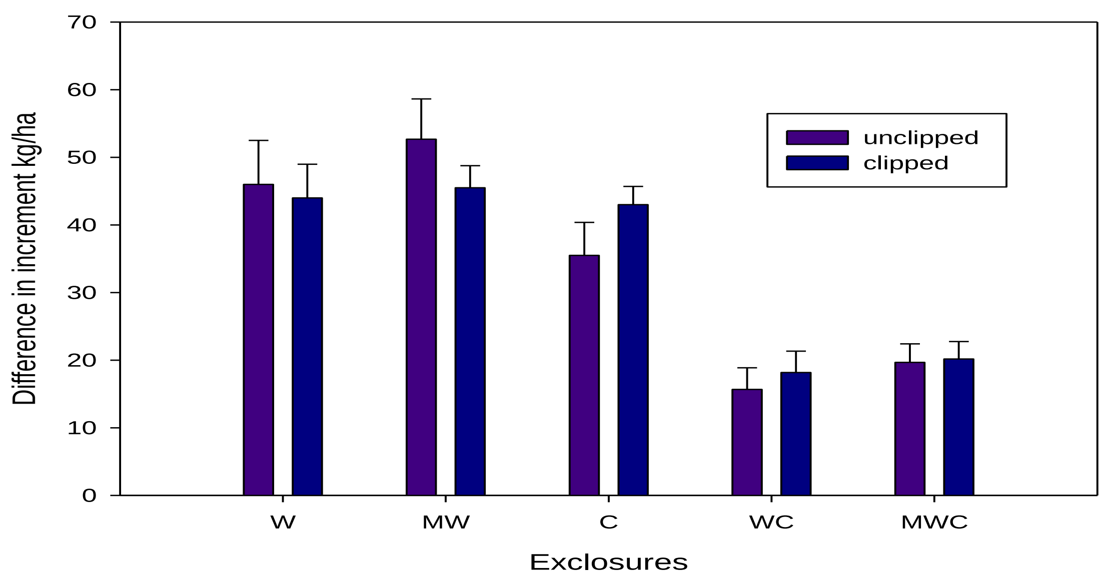

Figure 18. Difference in increment in forage biomass (Kg/ha/month) between caged plots with unclipped forage, caged plots with clipped forage and open grazed areas in the 2008 dry season (t_0 at beginning of December and t_1 at end of February 2008)

The results (Fig. 19) show slight differences in forage increment between clipped and caged and unclipped and caged plots in the exclosures grazed by cattle together with wild herbivores (WC and MWC), whereas large differences between clipped and caged and unclipped and caged plots in the ungrazed and exclosures grazed by wildlife (O, W and MW) during the wet season. The results indicate that clipped forage plants exhibit higher growth responses than unclipped plants. However, during the dry season, there were small differences in the increment of forage biomass between the clipped caged and unclipped caged plots due to lack of soil moisture.

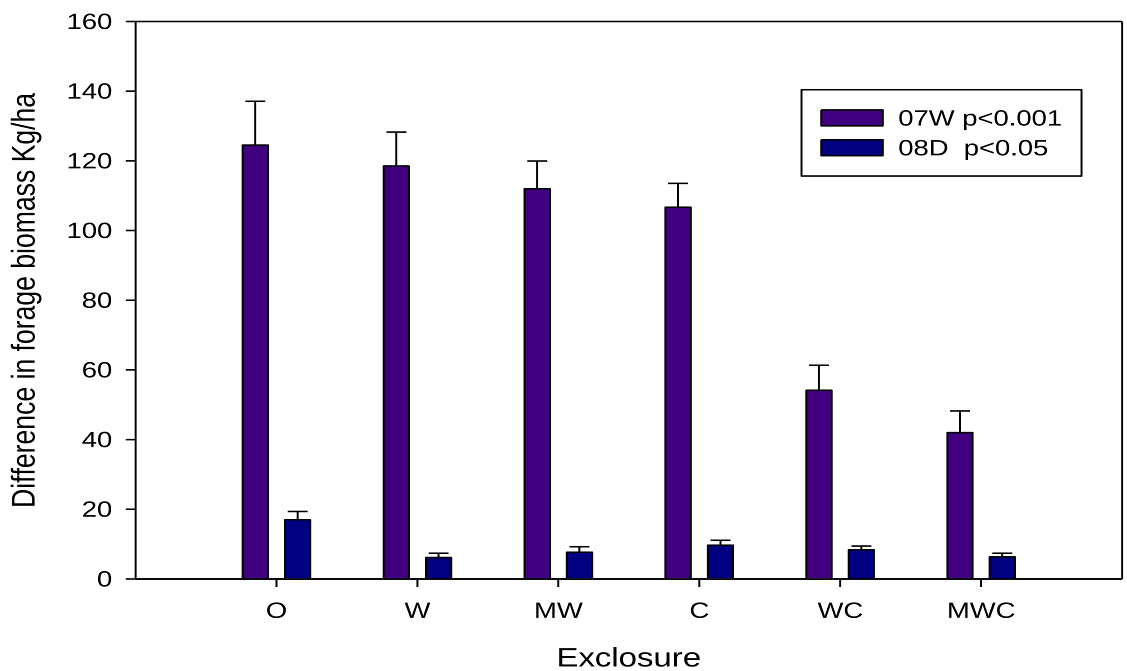

Figure 19. Difference in increment in forage biomass (Kg/ha/month) between clipped and caged and unclipped caged plots in the exclosures in the 2007 wet and 2008 dry seasons (August – October 2007 and December 2007 – February 2008)

Discussion

The effects of grazing by cattle and wildlife on forage biomass

Forage biomass in the exclosures was influenced by the type of herbivores grazing with a rapid decrease in forage biomass in exclosures grazed by cattle (Fig. 11). High stocking rates in the exclosures grazed by cattle increased grazing pressure on forage plants, especially on palatable plant species resulting in high decrease in forage biomass. Large amounts (4 %, 15 % and 17 %) of the total forage biomass were consumed in the exclosures grazed by cattle (C, WC and MWC) in the wet seasons and 9 %, 14 % and 16 % consumed in the dry season. Large amounts of forage were consumed because cattle are bulk grazers, able to utilize a grass sward to as low as 3 cm (Homewood & Rodgers 1991).

Non-selective grazing by cattle, due to wide mouth and flexible upper lips, take large amounts of forage (Lyons and Muchen 2002) reduced competition between the tall grasses, forbs and short grasses for light and soil nutrients, enhancing the growth of short grasses and forbs; *Brachiaria eruciformis*, *Aristida congesta*, *Eragrostis tenuifolia* and *Commelina erecta* by over 10 % (Chapter 2). The short nutritious grasses and forbs attracted small herbivores such as Grant's gazelles, hartebeest and dik diks to graze on the short grasses and forbs leading to further decrease in forage biomass in exclosure grazed by cattle (C, WC and MWC). Smaller grazers achieve energy requirements from short grasses compared to big herbivores (Prins & Olff 1998).

Conversely, only 5 % and 7 % of the total forage biomass were consumed in the exclosures grazed by wildlife (W and MW) in the wet seasons and 5 % and 6 % in dry season resulting in a small decrease in forage biomass in the pasture grazed by wild herbivores. The small amount of forage biomass consumed was attributed to low stocking rates of wildlife at the study site and selective grazing by wild herbivores leading to light defoliation of forage plants.

Light and moderate defoliation of grasses by wild herbivores may promote plant production by maintaining high leaf area per land unit area (Briske *et al.* 2008) and hence high forage biomass in the exclosures grazed by large wildlife. Grazing during early growth stages and flowering stage can trigger beneficial responses (Sinclair 1975) such as reducing senescent material that may inhibit new growth and removing apical dominance, thus stimulating tillering in grasses (Valentine 1990).

Browsing on trees and shrubs by the mega-herbivores, elephant and giraffe (non-ruminants) may also have contributed to high herbaceous forage biomass in the exclosures grazed by mega-wild herbivores (MW) (Fig. 11). For instance, studies carried out in the exclosures to assess the impact of mega-wild herbivores on tree density and herbaceous cover have indicated a reduction in density of dominant *Acacia drepanolobium* in plots in which the mega-herbivores had access and an increase in percentage cover of grasses and forbs, compared to high tree density in exclosures in which the mega-herbivores were excluded (Augustine & McNaughton 2004; Goheen *et al.* 2007; Pringle 2008; Riginos & Young 2007). Extensive browsing by elephants cause changes in the vegetation composition by opening up dense stands of shrubland and increasing the abundance, availability and forage production of the herbaceous layer (van Wijngaarden, 1985). Therefore, the results show that grazing by wildlife does not reduce forage biomass in the pasture and hence do not support the hypothesis that grazing by wildlife results in decrease in forage biomass on communal grazing lands.

The effects of grazing by cattle and wildlife on forage growth

Grazing and clipping of forage had an influence on growth of forage plants in a pasture as indicated by the variations in increment in forage biomass in the unclipped and caged, clipped and caged plots and open grazed areas (Figs. 13, 14 and 15). The large increment of forage biomass in caged plots in the grazed exclosures implies the importance of deferment grazing plans in a pasture. Deferment provides time for the grazed plants to recover from the effect of defoliation by herbivores and increases the growth potential of the residual foliage on the grazed plants. Defoliation through grazing and clipping enhances photosynthesis through removal of senescent tissues and increase in nutrient intake (Meyer 1998; Anten & Ackerly 2001). Defoliation by grazing also removes the dormancy of the apical buds and hence production of new shoots by the basal buds (Cable 1982). The slight increment in forage biomass in ungrazed exclosures (O) and exclosures grazed by wildlife (W and MW), an optimum increase in the exclosures grazed only by cattle (C) and ultimate decrease in exclosures grazed by cattle together with wildlife (WC and MWC) (Figs. 13 and 15) demonstrates that stocking rates have an influence on plant growth. Low stocking density (0.05 livestock units /ha) of wild herbivores in the exclosures grazed by wildlife alone (W and MW) leads to a small increment in forage biomass due to senescence of plant species. Similarly, high stocking densities (0.14 livestock units/ha) in the exclosures grazed by cattle (C) and (0.19 livestock units/ha) in the exclosures grazed by cattle with wildlife) result in small increments in forage biomass due to overgrazing reducing photosynthesis of the grazed plants. It is also possible that the 15-year history of experiments on the site has changed the vegetation to short statured vegetation type. The decrease in increment (low response) in forage biomass in the exclosures grazed by cattle together with wildlife (WC and MWC) may be explained by the decrease in the regenerative capacity of the forage plants due to heavy grazing, in which heavy grazing removed the growing points of tall grasses and forbs (Lyons & Hanselka 2003) or could be that these exclosures have switched to short-statured, productive species that do not produce as much standing biomass. Heavy grazing removes the elevated buds (growing points) of tall grasses, reducing new leaf production and the destruction of the buds inhibiting seed production and production of new seedlings (Lyons &

Hanselka 2003), whereas moderate stocking rates enhance plant growth resulting in high forage biomass. These findings are in agreement with the optimisation hypothesis of herbivory on herbaceous plant communities (McNaughton, 1979; 1983; Briske & Heitschmidt 1991) which suggests that optimal grazing intensity increases net primary production of a grazing system, while high stocking rates generally lead to reduced production through defoliation and damage caused by trampling (King *et al.* 1979; Binnie & Chestnutt 1991). Intensive grazing can enhance plant growth through the hormones secreted by herbivores (Hoogesteger & Karisson 1992). Furthermore, herbivores through urine and dung deposition can induce an increase in plant nitrogen content and maintain the grass in an immature, nitrogen-rich state (McNaughton 1985) since grazing accelerates nutrient recycling in the ecosystem and makes some nutrients more available (Valentine 1990).

The findings of this study which show that grazing pressure (grazing intensity) influences the response of forage plants as indicated in the grazed exclosures (Figs. 13, 14 and 15) are in contrast with the findings of Ferraro and Oesterheld (2002). The results highlight that moderate grazing (0.14 livestock units/ha in exclosures grazed by cattle only) increases forage production, whereas heavy grazing (stocking rates of >0.19 livestock units/ha as in exclosures grazed by cattle with wildlife) reduces forage production and hence decreases forage biomass in a pasture in semi-arid lands. Nevertheless, the results underline that high forage biomass in semi-arid lands can be sustained with appropriate moderate stocking rates of livestock and wild herbivores.

The small increments in forage biomass in the unclipped and caged plots in the ungrazed (O) exclosures were probably due to inter-specific plant competition. The herbaceous layer in the ungrazed exclosures comprised the dominant tall grasses and forbs (Chapter 2) that competed for light, soil moisture, nutrients and space reducing growth of less dominant plants, thus causing low increment in forage biomass in the wet season. However, low increment in the dry season was because of insufficient soil moisture, reducing plant growth. The results emphasize the impact of deferment (no grazing) on forage production in semi-arid lands.

The implications of grazing by livestock with wildlife on forage biomass

Intensive grazing by cattle with wildlife results in the decline in forage biomass in semi-arid lands. Heavy grazing may also lead to an increase in woody plants (bush encroachment) which can eliminate herbaceous plants by successfully competing with them for water (Bedell & Buckhouse 1994), thus reducing forage biomass. Decrease in forage biomass due to overgrazing may cause livestock to move long distances on rangelands looking for palatable forage plants, affecting forage intake and production (Ego *et al*. 2003). Conversely, the intensive browsing by mega-herbivores opens up wooded-grassland to open grassland (facilitation) that is beneficial to the grazing livestock (Bedell & Buckhouse 1994).

Conclusion

The response of forage biomass in semi-arid lands is dependent on the stocking rates (grazing intensity) and season and provides evidence that intensive grazing by cattle reduces forage biomass. This is because intensive grazing results in partial compensation (under compensation) by the forage plants, resulting in a decline in forage biomass. Although the results indicate that wild herbivores may have little effect on forage biomass available in the pasture, overstocking as a result of large herds of wild herbivores and livestock grazing on communal lands may lead to over-utilization of forage resources resulting in rangeland degradation. The findings of this study provide insight into the effect of grazing by wildlife and livestock on forage biomass in semi-arid lands. This information (knowledge) is fundamental for sustainable utilization of forage on communal grazing lands that should maintain moderate livestock stocking rates in order to integrate wildlife to enhance diversification in pastoral household income from livestock production and wildlife conservation activities without compromising the quality of rangeland resources.

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CHAPTER FIVE

Using faecal sampling to assess the effect of wildlife forage preference on cattle diet in semi-arid lands, Kenya

Abstract

There is a general view by ranchers and pastoralists that wildlife grazing deprives livestock of palatable forage plants, affecting nutritional quality of the diet of livestock on communal grazing lands and ranches. However, there is a lack of information which demonstrates that preference for forage plants by wild herbivores affect cattle diet in semi-arid lands in Kenya. This study estimated proportions of forage plants in the diets of wild herbivores and cattle in semi-arid lands where forage resources are shared by cattle and wildlife. The study was conducted on Mpala Ranch, Laikipia District, Kenya. Fresh faecal samples of cattle, zebra, hartebeest, oryx and Grant's gazelle were collected on the Ranch on which cattle graze together with wildlife. The samples were dried at room temperature, ground and analysed using micro-histological techniques to determine the composition of grass species, forbs and shrubs in the diet of cattle and wild herbivores. Faecal samples were also analysed for percentage crude protein and mineral contents in the diet of wild herbivores and cattle. The results indicate high proportions of tall coarse grasses in the diet of zebra and oryx, high proportions of forbs in the diet of hartebeest and Grant's gazelle and high propotions of short grasses in the diet of cattle which implied variations in forage preferences among grazing herbivores. The results also indicated a rapid decrease in crude protein contents in faecal samples of cattle and wild herbivores during the dry season. Although the results indicate a small (1%) overlap in plant species consumed between cattle and wild herbivores in the wet season, grazing by wildlife may not deprive cattle of essential nutrients because of high plant species diversity and high forage during the wet season.

Introduction

It is assumed that related animal species that live together show specialization in feeding to reduce competition for forage (Prins *et al.* 2006). However, wild herbivores and livestock may compete for scarce resources, especially in arid and semi-arid rangelands (Voeten & Prins 1999). The diet of livestock species and wild herbivores can overlap, because livestock has similar resource requirements to wild herbivores (Sitters *et al.* 2009). Shared grazing by cattle and wildlife may change feeding patterns, thus affecting the diet of cattle in semi-arid lands (Odadi *et al.* 2009). Generally, it is assumed that forage preferences that result in selective grazing and browsing by wild animals deprive cattle of some of the forage plants that are rich in nutrients, and the deficiency of these nutrients in a pasture compels cattle to move in search of nutritious plants, resulting in high energy expenditure that reduces livestock growth rates and thus causes low live weight gain (Ego *et al.* 2003). Selection of forage plants by coexisting herbivores is a prerequisite for understanding livestock-wildlife interactions, their impact on the vegetation communities (Persson *et al.* 2000; Suominen *et al.* 2008), as well as to predict their patch choice and spatial distribution (Kuijper & Bakker 2008). Data on dietary overlap may also be used by range/ranch managers to select animal species that may utilize a variety of forage plants in order to minimize foraging pressure on any particular plant species and thereby improve the stability of the plant-animal interaction on rangeland ecosystem (Murden & Risenhoover 1995). Although many examples indicate negative impacts of cattle grazing on wild ungulates, the effect of grazing by wild herbivores on cattle diet is not clear (Chaikina & Ruckstuhl 2006). General linear models can be used to solve resourse allocation problems such as allocating a limited forage supply to a guild of ungulate species in semi-arid lands (Kuzyk *et al.* 2009). In a multi-species system dry matter intake varies among herbivore species, but can be generalized from their digestive capacity and body size (van Soest 1994).

Diet selection by herbivores

Diet selection and hence forage consumed is influenced by herbivore species and body size (Lyons & Machen 2002). Each animal species selects and consumes plant species from a variety of forage plants on offer (Forbes 1986) that supply them with a high amount of energy and with nutrients needed to maintain their basic body functions (Schoener 1971). The diet selection and amount of food eaten depends on palatability of the plant, plant parts available and the accessibility of the plant species (Forbes 1986). Wild herbivores consumes forage that satisfies nutritional body requirement that make the animals feel satiated (Kleiber 1961; Stephen & Krebs 1986) and diet selection declines when foods are eaten to satiety (Provenza 1996a) (Fig. 20 g).

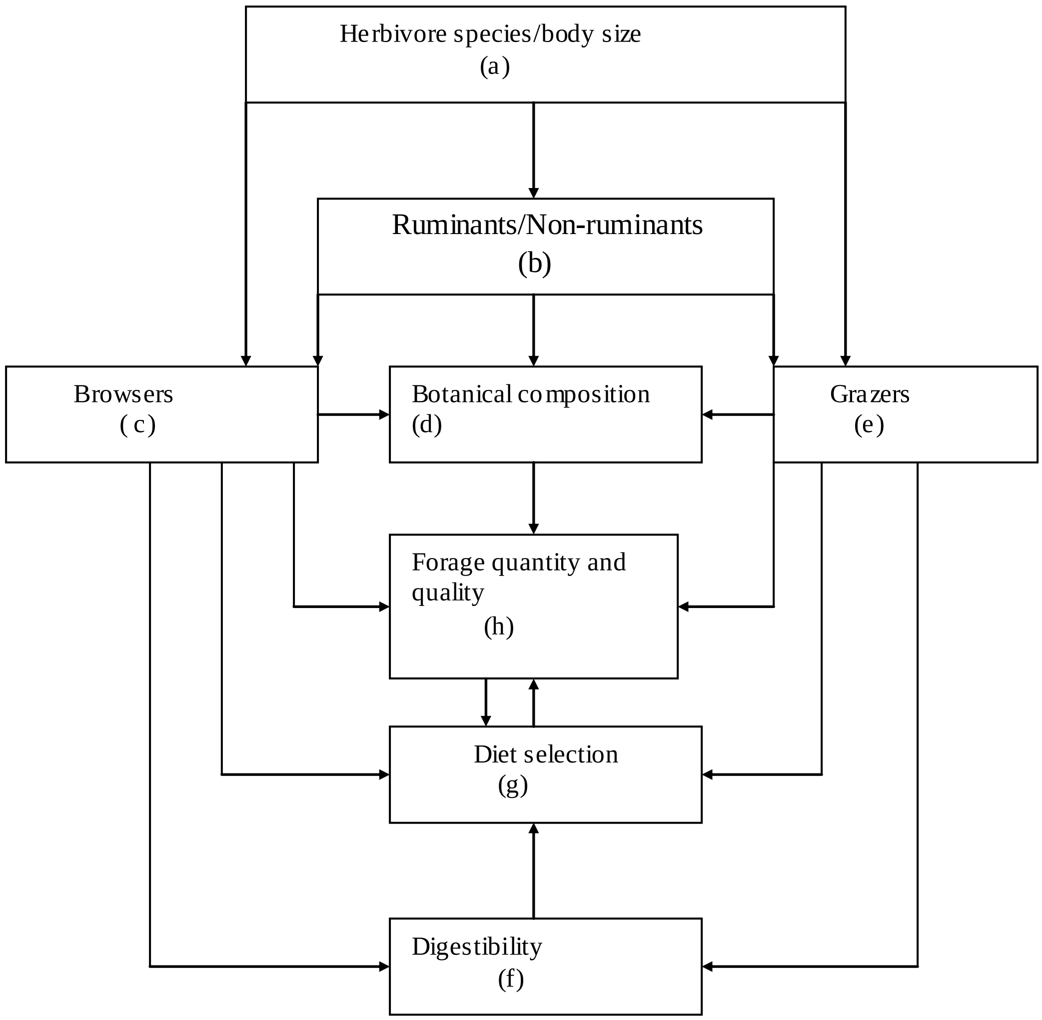

Figure 20: Factors influencing diet selection among herbivores. The arrows show the directions of the influence.

The influence of herbivore species and body size on diet selection

Grazing animals differ in the way they bite and ingest forage and these differences are related to the types of forage various animals prefer (Lyons & Machen 2002). Animal and rumen sizes have fundamental influence on animal metabolism and hence on animal energy needs thus larger animals ingest food of potentially lower nutritive value (Hodgson 1981) such as fibrous grasses, trees and shrubs (Demment & Van Soest 1985). The digestive system of a ruminant has a rumen and reticulum in which the bulk of fermentation occurs (Langer 1988; van Soest 1994) but a non-ruminant herbivores relies on an enlarged caecum where additional microbial fermentation occurs (Langer 1988) (Fig. 20 a).

The influence of grazers and browsers on diet selection

Strong preference for grasses by cattle (ruminant) contributes to the loss of palatable species such as *Themeda triandra* in semi-arid lands, thus depriving wildlife grazers of palatable grasses that influence the diet selection by wild herbivores (Andrew 1986). Feeding on coarse, less palatable grass species avoided by cattle (Langer 1988), zebra minimize competition for forage with cattle. In contrast, browsers tend to have prehensile lips and select specific plant parts that have less cell wall (Hofmann 1985). Browsing by elephants may suppress tree seedlings regeneration and recruitment, thus enhancement in germination of herbaceous forage plants for grazers (Prins and Van der Jeugd 1993) (Fig. 20 c and e).

The influence of botanical composition, quantity and quality on diet selection

Diet selection by a grazing animal is dependent on plant characteristics in the pasture (Hudson & Christofferson 1985). Diet selection is also determined by forage quality of plant species and hence grazing herbivores eating preferred plant species in greater proportions than less preferred plants (Petrides 1975; Grunow 1980; Mentis 1981). Digestible dry matter (energy), crude protein, and fibre contents of the forage (Sanderson & Wedin 1989; Mitchell *et al.* 2005) influence forage preference and diet selection by herbivores and thus as the energy, crude protein content in forage increases, intake of forage quantity increases (Lyons & Machen 2002). There is low preference for plants with high content of lignin and crude fibre but a positive relation between plant preference and sugars, proteins, fats and water soluble carbohydrates (Maryland *et al.* 2000b; Ciavarella *et al.* 2000) (Fig. 20 d and h).

The influence of digestibility on diet selection

The amount of forage consumed by ruminants and non-ruminants (critically important for the requisition of nutrients) depends on the amount of time spent grazing, the rate of consumption, capacity of the digestive tracts and the rate of breakdown of cellulose in the fibrous matter of the grass by bacteria and other micro-organisms (Ngugi *et al.* 1978; Rinehart 2008; Welch & Hooper 1988). The more rapidly the food is digested and passed through the animal the greater the potential for its consumption by grazing herbivores (Meissner 1999) (Fig. 20 f).

It was hypothesized that grazing by wildlife would affect cattle diet on rangelands. This is because of the assumption that forage preferences and selective grazing and browsing by wild animals deprive cattle of some of the forage plants that are rich in nutrients, and the deficiency of these nutrients in a pasture compels cattle to move in search of nutritious plants, resulting in high energy expenditure that reduces livestock growth rates and thus causes low live weight gain (Ego *et al.* 2003). It is also assumed that reduced cattle performance in arid and semi-arid lands is associated with reduced forage biomass and hence reduced forage intake (Prins 2000). Therefore, in view of knowledge gap on the effect of forage preference by wild herbivores on the diet of cattle in semi-arid lands, this study examined the impact of plant species utilization by wild herbivores on cattle diet in a semi-arid environment. The goal was to determine plant species consumed by zebra, hartebeest, oryx, Grant's gazelle and cattle to evaluate the actual proportions of forage plants in the diet of cattle and wild herbivores that may augment the competitive interactions between cattle and wild herbivores grazing together on communal grazing lands. The information on plants eaten by wild herbivores and cattle is vital because the diet of wild herbivores and livestock in semi-arid lands is selected from indigenous vegetation. The information of this study is to provide insight into the seasonal changes in the diets of wildlife and domestic herbivores by determining proportions of forage plants in the diets of wild herbivores and cattle.

Material and methods

Faecal sample collection

Fresh faecal samples from cattle, Grant's gazelle, oryx, zebra and hartebeest were collected on Mpala Ranch during the 2007 wet and 2008 dry seasons and dried at room temperature to minimise volatilization (vaporization) of nitrogen from the samples. There was no separation of faecal samples from the plain zebra and Grevy's zebra. Faecal nutrient constituents (crude protein and mineral), plant species composition were analysed as a compsite sample from the two zebra species without separation because the two species grazed in same area. However, 95 % of the zebra population on Mpala ranch are Burchell's zebra (*Equus burchelli*), whereas 5 % zebras are Grevy's zebra (*E. grevyi*) (Khaemba *et al.* 2001).

The dried samples were ground and packed in plastic bags for analysis for plant species composition, crude protein and mineral content to assess the nutritional quality of forage ingested food by wild herbivores and cattle. Faecal samples slides were prepared and examined under a compound microscope and the plant species consumed by herbivores identified. Wild herbivores eat a great variety of plant species and plant parts and reliable estimates of their protein intakes cannot be made from herbage samples because of diet selectivity among herbivores (Arman *et al.* 1975).

Although elephant and giraffe were present at the study site, faecal samples were not collected because they were mainly browsers, the elephant feeding on barks, branches and leaves of trees and shrubs and giraffe feeding on leaves of acacia trees and shrubs, thus high variation in diet between browsers and cattle (grazer). The selection of zebra, oryx, hartebeest and Grant's gazelle was based on high population or numbers of these herbivores at the study site (exclosures). For example, on Laikipia rangelands there are 148,850 zebras; 53,700 oryx; 93,800 hartebeest and 247,500 Grant's gazelles (Ottichilo 2000a) representing over 43% of the total (1,262,400) wildlife population. This high population (>43 %) of wildlife grazers and mixed feeders on Laikipian rangelands was likely to have an effect on herbaceous forage biomass compared to low population densities of buffalo (35,450) and less than 35, 000 elephants in Kenya (which constitute only 6 % of the total wildlife population on Kenyan rangelands) and may have less effect on the herbaceous layer at the study site. The elephant and buffalo populations on Mpala ranch are very low (less than 2 % and less than 5 % respectively) of the total population on Kenyan rangelands.

Preparation of slides from reference plant and faecal samples

Reference slides were prepared from plant species (herbaceous plant species and shrubs) collected within Mpala Ranch. The fresh plant materials of each plant species was immersed in a bottle containing a mixture of formalin-acetic-alcohol (850 ml 70 % alcohol, 100 ml 40% formaldehyde and 50 ml glacial acetic acid) to preserve its shape and size and render the tissues suitable for sectioning (Cavender & Hansen 1970). The reference slides were used to aid in identification of the plant species consumed by herbivores by comparing similarities in structures of hairs and papillae (trichomes) on fragments in the faecal samples with those on reference plants because hairs are characteristic of particular plant species. The variation in structure of the epidermal hairs among plant species facilitates the identification of various plant species and this method has been used in many studies (Hercus 1960; Steward 1967; Olsen and Hansen 1977; Mbatha and Ward 2006).

Three faecal samples each from cattle, zebra, oryx, hartebeest and Grant's gazelle in 2007 wet and 2008 dry seasons and 9 herbage samples were collected on different parts of the ranch in the 2007 wet and 2008 dry seasons. The samples were oven-dried at 60°C for 48 hours and then ground to pass through a 0.5 mm sieve. One tablespoonful of each of the faecal sample was soaked in hot water for 10 minutes to soften cell tissues, drained and rinsed in cold water. Plant pigments were removed with a 4 % sodium hypochlorite solution that dissolved chlorophyll to render the features of epidermis and cuticle visible. Four slides were prepared from each herbivore faecal sample and twenty-five microscope fields of view were examined on each of the four slides of each herbivore faecal sample (i.e. total of 100 fields examined). A movable stage microscope with 100X magnification was used to identify plant fragments in faecal samples and the identifiable plant fragments at each location (in each field) were counted and the relative percentage frequency of each species determined (Sparks & Malechek 1968; Foppe 1984; Hansen & Clarks 1984). Fragment counts were used to quantify species composition of grasses and non-grasses in individual faecal samples (Stewart & Stewart 1970). Relative density (RD) of each plant species was calculated using the formula of Hansen & Clarks (1984):

$$\text{R. D.} = \frac{\text{Density of discerned fragments for a species}}{\text{Density of discerned fragments of all species}} \times 100$$

Plant species composition in the pasture was determined by the frequency of each plant species i.e. measurements were taken at 100 sampling points along transect lines. Frequencies of herbaceous plant species were determined by the formula:

$$f = \frac{\text{number of points at which plant species occurred}}{\text{Total number of points examined}} \times 100$$

where f is the percentage frequency of each plant species.

Faecal and forage sample nutrient analysis

The analysis of nutrient contents in forage and faecal samples of cattle and wild herbivores was done at the Animal Feeding Resource for Eastern Africa (AFREA) Laboratory, Egerton University, Kenya, using official (AOAC 1990) methods of crude protein and mineral content as described in the procedure below.

Mineral content determination

The percentage mineral content included all the micro and macro nutrients: phosphorus, calcium, magnesium, sodium and silica. Dried and ground forage and faecal samples were weighed on an analytical balance and put in dry weighed crucibles. The crucibles and the contents were put in an incinerator (Muffle furnace) at 550° C for 3 hours. After incinerating, the contents were removed and allowed to cool in a dessicator to room temperature and weighed. The net mass contents after incineration was the mass of mineral, while the loss in mass constituted the volatile portion of the sample, which included the nitrogen and carbon (AOAC 1990).

$$\% \text{ Ash} = \frac{(H-C)}{(D-C)} \times 100$$

where; C is mass (g) of empty crucible

D is mass (g) of crucible + sample

H is mass (g) of crucible + residue.

The ash value constituted the inorganic (mineral) portion of the sample.

Determination of crude protein in the diet

Three grams of ground, oven-dried forage and faecal samples were used for the analysis of percentage crude protein (% CP). Crude protein content was analysed using Kjeldahl procedure (AOAC 1990). Value of crude protein in the sample was estimated by multiplying the nitrogen content by 6.25. Determination of crude protein content in the diet of herbivores is important because crude protein establishes the quality of forage consumed by herbivores.

Data analysis

Transformation of the percentage utilization of the dominant grasses

The percentage frequency of each of the six dominant grasses and forbs in the diet was calculated from the 100 microscope fields examined and converted into a ratio of proportions (p) and the data transformed into log-odds values, i.e. $\hat{Y} = \log\left(\frac{p}{1-p}\right)$ (Dayton 1992). The transformation of data into log-odds was to meet the assumptions for the linear models. The log-odds values were used in the linear regression to assess the effect of the presence and grazing by wild herbivores on proportions of forage plant species in the diet of cattle. The dominant grasses and forbs were selected because of high composition in the pasture and hence availability to the grazing herbivores. The effect of grazing by wildlife and cattle on forage plants in the diet was determined using a logistic regression model:

$\hat{Y}$= c + h + g + o + z

Where: $\hat{Y}$ is the log-odds (proportions) of grass and forb species in the diet (dependent variable); ‘c’ indicates presence of cattle in pasture; ‘h’ indicate presence of hartebeest in the pasture and ‘g’ indicate presence of Grant’s gazelle in the pasture; ‘o’ indicate presence of oryx in the pasture and ‘z’ indicate presence of zebra in the pasture (independent variables).

In the current study, general linear models are used to show the estimated proportions of forage plants in the diets of wild herbivores and cattle which may reflect the intensity of forage utilization and approximate the dry matter intake of each dominant grass species based on the body size (live-weights) of cattle and wild herbivores. Competitive interaction between cattle and wild herbivores is influenced by the amount of forage consumed and the forage biomass available in the pasture. The effect of grazing by wildlife on diet of livestock in semi-arid lands is influenced by amount of forage intake by cattle and wild herbivores. Dry matter intake by cattle and wild herbivores was estimated by multplying the proportions of dominant grass and forb species in the diet and 3 % of the body weight (equivalent to dry matter intake by mature herbivores) to compare differences in amounts of forage consumed. Overlap in proportions in diets between cattle and wildlife may not provide evidence of competition for forage as forage biomass available may influence amount of forage consumed.

Statistical Package for Social Sciences (SPSS version 11.5) computer software was used for linear regression analysis of independent variables (c + h + g + o + z) against the log-odds of the percentage frequencies of grasses and forbs in the diet (dependent variable). The inverse of the log of the coefficients of the estimates of the best fit regression line, i.e. $e^{(\hat{Y})}$ were used to calculate the proportions of grass and forb species in the diet of wild herbivores and cattle. The proportion of each grass and forb species was determined using the formula:

$$x = \left(\frac{p}{1-p}\right); \; x - xp = p$$

$$x = p\,(1 + x)$$

$$x = p + xp$$

$$\frac{x}{1+x} = p$$

where: x is the exponential of the log-odds ($e^{(\hat{Y})}$) of the grass and forb species and p is the proportions of grass and forb species in the diet of cattle and wildlife (c + h + g + o + z). Regression analysis was done using SPSS computer software whereby the log odds of the frequencies of grass and forb species in the diets of cattle and wild herbivores were entered and the anti-log of the coefficients in the regression model for cattle (reference animal) and wild herbivores were used to determine the proportions of grass and forb species in the diet. Pearson bivariate correlation analysis (using SPSS version 11.5) was also done to determine the overlap in the proportions in the diet between cattle and wild herbivores.

Results

Proportions of grass species and forbs in the faecal samples of herbivores

The results of regression models (Table 8 and 9) show the proportions of dominant grass and forb species in the diets of cattle, hartebeest, Grant's gazelle, oryx and zebra grazing in the pasture. Cattle were clearly distinct from other wildlife in terms of their ingestion of a few of key species particularly *Themeda triandra* (5 – 8 %) more prevalent in cattle than in other wildlife and *Brachiaria lachnantha* (4 – 8 %) less prevalent in cattle diet than in other wildlife. The pattern of *Themeda triandra* changed during the dry season when wildlife also started depending more on this palatable species. Cattle still had a large proportion of *Themeda triandra* in the diet but the proportion of *Lintonia nutans* also increased in the dry season. The results indicate high ingestion of *B. lachnantha, Pennisetum stramineum and P. mezianum* by wildlife with 4 – 14 % more in the diet compared to the diet of cattle --- an indication of selection of palatable species by cattle. There is slightly higher intake of *Rynchosia nyasica, Rhinacanthus ndorensis, Hibiscuss flavifolius* and *Commelina erecta* by hartebeest and Grant's gazelle with 1 – 4 % more in the diet compared to the diet of cattle but 1 – 6 % less in the diets of oryx and zebra in the 2007 wet season, thus low intake of forbs by oryx and zebra. Similarly, in the 2008 dry season there was a high intake of *Rhinacanthus ndorensis* and *Indigofera schimperi* by hartebeest and Grant's gazelle with 3 – 7 % more in the diet compared to the diet of cattle. However, there diets of oryx and zebra had 2 – 8 % less in the diet comapared to the diets of cattle, hartebeest and Grant's gazelle (Table 9).

Table 8: Estimates of the proportions of the dominant grass species in the diet of cattle, hartebeest, Grant's gazelle, oryx and zebra grazing together in the pasture (L = lower limit; U = upper limit at 95% confidence interval: calculated by 2 x SE). SE=standard error.

Season/grass species/ herbivore type 2007 wet season	Coefficient (β)	SE	95 % C.I.		% estimates of proportions of grasses in diet of herbivores	df	F	T	Sign	R^2
Brachiaria lachnantha			Bl (L)	Bl (U)						
Cattle	0.602	0.182	0.238	0.964	65	99	29.486	7.238	0.0001	
Hartebeest	0.841	0.112	0.617	1.065	70			4.154	0.0001	
G. gazelle	0.980	0.124	0.732	1.228	73			3.470	0.0001	0.931
Oryx	0.805	0.165	0.475	1.135	69			5.991	0.0001	
Zebra	0.874	0.188	0.498	1.250	71			8.980	0.0001	
Pennisetum stramineum			Ps (L)	Ps (U)						
Cattle	0.571	0.232	0.107	1.035	64	99	19.261	4.656	0.0001	
Hartebeest	0.525	0.173	0.179	0.871	63			3.144	0.0001	
G. gazelle	0.560	0.210	0.140	0.980	64			3.433	0.0001	0.903
Oryx	0.746	0.162	0.422	1.070	68			4.253	0.0001	
Zebra	0.790	0.347	0.096	1.484	69			5.302	0.0001	
Pennisetum mezianum			Pm (L)	Pm (U)						
Cattle	0.385	0.171	0.043	0.727	60	99	14.380	6.197	0.0001	
Hartebeest	0.348	0.095	0.158	0.538	59			3.841	0.001	
G. gazelle	0.470	0.078	0.214	0.626	62			6.513	0.0001	0.885
Oryx	0.625	0.263	0.099	1.151	65			6.860	0.0001	
Zebra	0.703	0.241	0.221	1.185	67			7.310	0.0001	

Themeda triandra			Tt (L)	Tt (U)						
Cattle	0.991	0.097	0.797	0.185	73	99	21.986	7.530	0.0001	
Hartebeest	0.601	0.170	0.261	0.941	65			5.421	0.0001	
G. gazelle	0.615	0.148	0.319	0.911	65			5.359	0.0001	0.917
Oryx	0.695	0.141	0.413	0.977	67			6.745	0.0001	
Zebra	0.770	0.114	0.542	0.998	68			7.149	0.0001	
Lintonia nutans			Ln (L)	Ln (U)						
Cattle	0.639	0.176	0.387	0.891	65	99	18.520	3.441	0.001	
Hartebeest	0.718	0.187	0.344	1.092	67			0.966	0.0001	
G. gazelle	0.695	0.122	0.451	0.939	66			2.699	0.0001	0.825
Oryx	0.682	0.218	0.246	1.118	66			4.642	0.0001	
Zebra	0.522	0.187	0.148	0.896	63			5.428	0.0001	
Bothriochloa insculpta			Bi (L)	Bi (U)						
Cattle	0.631	0.116	0.399	0.863	65		13.561	4.836	0.0001	
Hartebeest	0.620	0.227	0.116	1.074	65			3.992	0.0001	
G. gazelle	0.578	0.201	0.176	0.980	66			4.980	0.0001	0.816
Oryx	0.469	0.148	0.173	0.762	62			3.218	0.0001	
Zebra	0.335	0.174	0.013	0.683	58			3.439	0.001	

2008 dry season

Brachiaria lachnantha			Bl (L)	Bl (U)						
Cattle	0.695	0.143	0.409	0.981	66	99	38.973	9.665	0.0001	
Hartebeest	0.885	0.227	0.431	1.339	71			5.240	0.0001	
G. gazelle	0.920	0.121	0.678	1.162	72			5.137	0.0001	0.913
Oryx	0.948	0.065	0.818	1.078	72			5.677	0.0001	
Zebra	0.990	0.186	0.618	1.362	73			7.338	0.0001	

										Ps (U)
Pennisetum stramineum			Ps (L)	Ps (U)						
Cattle	0.248	0.153	0.058	0.552	56	99	34.362	5.245	0.0001	
Hartebeest	0.584	0.085	0.414	0.754	64			7.159	0.0001	
G. gazelle	0.636	0.092	0.352	0.820	65			6.410	0.0001	
Oryx	0.643	0.146	0.351	0.935	66			7.828	0.0001	0.936
Zebra	0.940	0.184	0.572	1.308	71			8.291	0.038	
						Pm (U)				
Pennisetum mezianum			Pm (L)	Pm (U)						
Cattle	0.325	0.127	0.071	0.579	58	99	22.249	6.358	0.0001	
Hartebeest	0.491	0.060	0.371	0.611	62			6.524	0.0001	
G. gazelle	0.389	0.095	0.199	0.579	60			6.081	0.0001	0.931
Oryx	0.755	0.195	0.365	1.145	68			7.178	0.0001	
Zebra	0.960	0.312	0.328	1.592	72			7.562	0.001	
Themeda triandra			Tt (L)	Tt (U)						
Cattle	0.906	0.167	0.542	1.280	71	99	24.760	7.250	0.0001	
Hartebeest	0.820	0.056	0.708	0.932	69			6.714	0.0001	
G. gazelle	0.910	0.041	0.828	0.992	71			7.180	0.0001	0.899
Oryx	0.865	0.109	0.647	1.083	66			5.731	0.0001	
Zebra	0.975	0.158	0.659	1.291	73			7.690	0.0001	
Lintonia nutans			Ln (L)	Ln (U)						
Cattle	0.963	0.198	0.567	1.359	73	99	23.963	8.175	0.0001	
Hartebeest	0.628	0.227	0.174	1.082	65			5.426	0.0001	
G. gazelle	0.569	0.273	0.023	1.115	64			5.380	0.0001	0.892
Oryx	0.695	0.276	0.143	1.247	67			6.062	0.0001	
Zebra	0.740	0.204	0.332	1.148	68			6.248	0.0001	

Bothriochloa insculpta			Bi (L)	Bi (U)						
Cattle	0.591	0.212	0.167	0.015	64	14.58		5.950	0.0001	
Hartebeest	0.480	0.171	0.138	0.822	62			3.802	0.001	
G. gazelle	0.572	0.184	0.204	0.940	64			5.629	0.0001	
Oryx	0.613	0.183	0.247	0.979	65			6.180	0.0001	0.810
Zebra	0.420	0.212	0.200	0.640	60			3.368	0.0001	

Table 9: Estimates of the proportions of forbs in the diet of cattle, Grant's gazelle, hartebeest, oryx and zebra (L= lower limit; U = upper limit at 95% confidence interval)

Season/grass species/ herbivore type 2007 wet season	Coefficient (β)	SE	95 % confidence interval		% estimates of the proportions of forbs in the diet of herbivores	df	F	T	Sign	R^2
Rhynchosia nyasica			Ryn (L)	Ryn (U)						
Cattle	0.296	0.085	0.126	0.466	57	99	10.840	4.725	0.001	
Hartebeest	0.318	0.140	0.038	0.598	58			4.937	0.001	
G. gazelle	0.345	0.090	0.165	0.525	59			4.017	0.001	0.701
Oryx	0.120	0.043	0.034	0.206	53			3.469	0.002	
Zebra	0.052	0.003	0.046	0.058	52			3.251	0.004	
Rhinacanthus ndorensis			Rndo (L)	Rndo (U)						
Cattle	0.212	0.101	0.010	0.414	55	99	23.996	4.591	0.0001	
Hartebeest	0.261	0.116	0.029	0.493	56			4.902	0.0001	
G. gazelle	0.280	0.100	0.080	0.480	57			4.895	0.0001	0.830
Oryx	0.165	0.056	0.043	0.277	54			3.526	0.001	
Zebra	0.151	0.068	0.015	0.287	54			4.565	0.001	

Hibiscus flavifolius			Hf (L)	Hf (U)						
Cattle	0.410	0.110	0.190	0.630	60	99	34.914	6.820	0.0001	
Hartebeest	0.425	0.119	0.187	0.663	61			7.158	0.0001	
G. gazelle	0.360	0.126	0.108	0.612	59			6.641	0.0001	0.915
Oryx	0.193	0.080	0.033	0.353	55			4.830	0.0001	
Zebra	0.330	0.063	0.184	0.456	58			5.626	0.0001	
Indigofera schimperi			Is (L)	Is (U)						
Cattle	0.340	0.107	0.126	0.554	58	99	49.189	8.954	0.0001	
Hartebeest	0.310	0.103	0.104	0.516	58			9.263	0.0001	
G. gazelle	0.362	0.108	0.046	0.678	59			9.146	0.0001	0.927
Oryx	0.112	0.032	0.048	0.176	53			6.812	0.0001	
Zebra	0.065	0.021	0.023	0.107	52			5.874	0.0001	
Commelina erecta			Ce (L)	Ce (U)						
Cattle	0.365	0.068	0.229	0.501	59	99	34.919	6.095	0.0001	
Hartebeest	0.517	0.078	0.361	0.673	63			7.721	0.0001	
G. gazelle	0.420	0.103	0.214	0.626	60			7.083	0.0001	0.875
Oryx	0.284	0.105	0.074	0.494	57			4.836	0.0001	
Zebra	0.195	0.056	0.083	0.307	55			3.710	0.001	
2008 dry season										
										Ps (U)
Rynchosia nyasica			Ryn (L)	Ryn (U)						
Cattle	0.435	0.141	0.153	0.717	61	99	22.310	5.883	0.0001	
Hartebeest	0.510	0.150	0.200	0.820	62			5.940	0.0001	
G. gazelle	0.545	0.116	0.313	0.777	63			5.182	0.0001	0.817
Oryx	0.353	0.108	0.137	0.569	59			3.960	0.001	
Zebra	0.105	0.046	0.013	0.197	53			3.112	0.001	

						Pm (U)				
Rhinacanthus ndorensis			Rndo (L)	Rndo (U)						
Cattle	0.325	0.123	0.079	0.571	58	99	9.371	3.109	0.001	
Hartebeest	0.608	0.129	0.350	0.866	65			4.641	0.001	
G. gazelle	0.569	0.106	0.357	0.781	64			4.529	0.001	0.712
Oryx	0.218	0.082	0.057	0.382	55			2.677	0.005	
Zebra	0.152	0.066	0.020	0.284	54			2.582	0.008	
Hibiscus flavifolius			Hf (L)	Hf (U)						
Cattle	0.599	0.093	0.413	0.785	65	99	19.259	5.420	0.0001	
Hartebeest	0.410	0.074	0.262	0.558	60			4.082	0.0001	
G. gazelle	0.505	0.062	0.371	0.639	62			4.635	0.0001	0.815
Oryx	0.321	0.082	0.157	0.485	58			3.149	0.001	
Zebra	0.345	0.123	0.099	0.591	59			3.530	0.001	
Indigofera schimperi			Is (L)	Is (U)						
Cattle	0.450	0.099	0.252	0.648	61	99	22.758	4.322	0.0001	
Hartebeest	0.675	0.096	0.483	0.867	65			5.938	0.0001	
G. gazelle	0.552	0.117	0.318	0.786	64			5.626	0.0001	0.830
Oryx	0.213	0.073	0.067	0.359	55			3.370	0.002	
Zebra	0.095	0.013	0.069	0.121	63			4.582	0.001	
Commelina erecta			Ce (L)	Ce (U)						
Cattle	0.128	0.034	0.68	0.196	53	99	8.334	3.529	0.001	
Hartebeest	0.100	0.019	0.062	0.138	53			3.381	0.001	
G. gazelle	0.145	0.012	0.121	0.169	54			3.610	0.001	0.690
Oryx	0.063	0.003	0.057	0.069	54			3.598	0.001	
Zebra	0.035	0.004	0.027	0.043	52			3.174	0.005	

Dry matter intake by herbivores

Dry matter intake of the grass and forb species was estimated on the basis of the proportions in the diets and liveweight (3 % body weight) of cattle and wild herbivores. Grazing by Grant's gazelle with a small body weight had the least effect on forage biomass of grass and forb species (<1kg DM intake) (Table 10, 11, 12 and 13). On the basis of dry matter intake by live-weights, 20 livestock units of cattle will be supported by removal of 1 mature elephant from the pasture, 1 mature bufallo will support 2 units of cattle and 1 zebra will support 0.7 units of cattle in the pasture, whereas the removal of 1oryx, 1 hartebeest and 1 Grant's gazelle will support less than 0.5 livestock unit in the pasture.

Table 10: Dry matter intake (kgs) of grass species based on proportions in the diet and liveweight of herbivores in 2007 wet season

Plant species	Grazing herbivores				
	Cattle	Zebra	Oryx	Hartebeest	G. gazelle
B. lachnantha	5.85	4.26	2.07	2.80	1.10
P.stramineum	5.76	4.14	2.04	2.52	0.96
P. mezianum	5.40	4.02	1.95	2.36	0.93
T. triandra	6.57	4.08	2.01	2.60	0.98
L. nutans	5.85	3.78	1.98	2.68	0.99
B. insculpta	5.85	3.48	1.86	2.60	0.99

Table 11: Dry matter intake (kgs) of grass species based on proportions in the diet and liveweight of herbivores in 2008 dry season

Plant species	Grazing herbivores				
	Cattle	Zebra	Oryx	Hartebeest	G. gazelle
B. lachnantha	5.94	4.38	2.16	2.84	1.08
P.stramineum	5.04	4.26	1.98	2.56	0.98
P. mezianum	5.22	4.32	2.04	2.48	0.90
T. triandra	6.39	4.38	1.98	2.76	1.07
L. nutans	6.57	4.08	2.01	2.60	0.96
B. insculpta	5.76	3.60	1.95	2.48	0.96

Table 12: Dry matter intake (kgs) of forb species based on proportions in the diet and liveweight of herbivores in 2007 wet season

Plant species	Grazing herbivores				
	Cattle	Zebra	Oryx	Hartebeest	G. gazelle
R. nyasica	5.13	3.12	1.59	2.32	0.89
R. ndorensis	4.95	3.24	1.62	2.24	0.86
H. flavifolius	5.40	3.48	1.65	2.44	0.89
I. schimperii	5.22	3.12	1.59	2.32	0.89
C. erecta	5.31	3.30	1.71	2.52	0.90

Table 13: Dry matter intake (kgs) of forb species based on proportions in the diet and liveweights of herbivores in 2008 dry season

Plant species					
	Cattle	Zebra	Oryx	Hartebeest	G. gazelle
R. nyasica	5.49	3.18	1.77	2.48	0.95
R. ndorensis	5.22	3.24	1.65	2.60	0.96
H. flavifolius	5.85	3.54	1.74	2.40	0.93
I. schimperii	5.49	3.78	1.65	2.60	0.96
C. erecta	4.77	3.12	1.62	2.12	0.96

There was no significant correlation (overlap) in the proportion of grass species in the diet of cattle and wild herbivores whereas there was a highly significant correlation (overlap) in the proportion of grass species in the diet of oryx and zebra and a highly significant overlap in the proportion of grass species in the diet of hartebeest and Grant's gazelle in the wet season as indicated by p-values (Table 14). Similarly, in the dry season there were no significant overlap in the proportion of grass species in the diet of cattle and wild herbivores. However, there was a very highly significant overlap in the proportion of grass species in the diet of hartebeest and Grant's gazelle (Table 15). There were no correlations (overlap) in the proportion of forbs in the diet of cattle and wild herbivores in the wet and dry seasons but a siginificant correlation in the proportion of forb species in the diet of hartebeest and Grant's gazelle in the dry season. The results imply that there is no evidence that grazing by wild herbivores has an effect on intake of grass and forb species by cattle.

Table 14: Pearson's bivariate correlation coefficient matrix (n = 6, df = 5) derived from table of proportions of grass species in diet of cattle and wild herbivores in wet season (p-values).

	Cattle	Zebra	Oryx	Hartebee	G. gaz
Cattle	-				
Zebra	0.880	-			
Oryx	0.699	0.010	-		
Hartebeest	0.417	0.881	0.467	-	
G. gazelle	0.737	0.619	0.394	0.012	-

Table 15: Pearson's bivariate correlation coefficient matrix (n =6, df = 5) derived from table of proportions of grass species in diet of cattle and wild herbivores in dry season (p-values)

	Cattle	Zebra	Oryx	Hartbeest	G. gaz
Cattle	-				
Zebra	0.921	-			
Oryx	0.935	0.266	-		
Hartebeest	0.307	0.224	0.188	-	
G. gazelle	0.351	0.456	0.411	0.005	-

Table 16: Pearson's bivariate correlation matrix (n = 6, df = 5) derived from table of proportions forb species in diet of cattle and wildlife in wet season (p-values).

	Cattle	Zebra	Oryx	Hartbeest	G. gaz
Cattle	-				
Zebra	0.301	-			
Oryx	0.394	0.249	-		
Hartebeest	0.067	0.314	0.075	-	
G. gazelle	0.780	0.778	0.058	0.242	-

Table 17: Pearson's bivariate correlation matrix (n = 5, df =4) derived from table of proportions forb species in diet of cattle and wildlife in dry season (p-values).

	Cattle	Zebra	Oryx	Hbeest	G. gaz
Cattle	-				
Zebra	0.129	-			
Oryx	0.058	0.280	-		
Hartebeest	0.351	0.838	0.390	-	
G. gazelle	0.173	0.457	0.121	0.04	-

Dietary nutrient contents

The percentage crude protein (% CP) levels in the diets of wild herbivores and cattle in the dry season ranged between 2.75 and 6.75 %, which is below 7 – 8%, the minimum % CP required to maintain rumen fermentation, implying consumption of low quality forage. Zebra diet contained the least % CP content in the wet and dry seasons, an indication of intake of plants with low crude protein content in the pasture. The percentage crude protein in the diets of herbivores reflected crude protein content in the forage on Mpala Ranch (Table 18). However, there were high concentrations of mineral in the diets of herbivores compared to content in the forage (Table 19), implying supplement of mineral in the diets of herbivores.

Table 18: Seasonal variation in percentage crude protein and mineral contents in faecal samples of wild herbivores and cattle

	% Faecal nutrient contents (Wet season)		% Faecal nutrient content (Dry season)	
Herbivore type	% CP	% Mineral	% CP	% Mineral
Hartebeest	7.25	22.25	6.75	32.75
Grant's gazelle	7.5	22	6.75	32.25
Oryx	6.0	20.25	4	31.25
Zebra	4.5	21.25	2.75	33.25
Cattle	7.0	23.25	4.25	33.0

Table 19: Seasonal variation in percentage crude protein and mineral contents in herbaceous forage samples on Mpala Research ceantre

	Wet season		Dry season	
Sampling points	% CP	% Mineral	% CP	% Mineral
1	7.09	12.52	6.86	12.94
2	3.95	12.72	3.74	15.09
3	3.85	11.27	2.61	12.38
4	8.70	10.88	8.17	11.00
5	7.76	9.70	6.16	12,08
6	6.60	11.30	5.28	11.82
7	6.34	10.48	5.35	10.91
8	6.60	15.40	5.59	15.45
9	8.33	11.30	7.45	11.82
Mean	**6.58**	**11.73**	**5.69**	**12.61**

Discussion

Proportions of grass species and forbs in the diets of herbivores

Although the high proportions of grass species in the diet of cattle and the diets of wild herbivores indicate high diet overlap, there is no evidence that grazing by wild herbivores had reduced forage biomass available that would result in competition for forage between cattle and wildlife affecting forage intake and hence poor cattle performance. Competition may arise where species reduce shared food resources to levels below which they cannot be efficiently exploited by other species (Illius & Gordon 1992) and forage resources are limited (Wiens 1989). On the basis of 3 % dry matter intake by body weight of herbivores (Pratt & Gwynne 1977) there was high intake of dry matter of grass species by cattle and zebra (Tables 5 and 6) which may lead to a rapid decrease in grass cover and biomass in the pasture especially during the dry seasons with a consequent competition for grass between cattle and zebra with almost similar body weight. However, there is no evidence from this study that indicate there was a limitation in the availability of herbaceous forage plants and forage biomass (Chapters 2 and 4) and therefore grazing by wild herbivores had no effect on cattle diet as generally assumed. The high dietary overlap between cattle and wild herbivores was probably because of abundance of grasses in the pasture. The dominant grass species comprise over 80 % herbaceous layer (Chapter 2). Nevertheless, size of grazing herbivore has a major influence on the level of voluntary feed intake (Allison 1985; Freer 1981) and hence possibility of competition for forage among grazing herbivores, particularly during dry season when there is scarcity of palatable forage plants. Competiton for forage between cattle and large wildlife may be minimal in the wet season due to high plant species diversity and forage biomass as indicated in Chapters 2 and 4. Forage quantity and quality is highest in wet seasons in semi-arid areas (Otieno 2004). Furthermore, high proportions of *P. stramineum* and *P. mezianum* in the diet of oryx and zebra in the wet and the dry seasons implies increase in consumption of the tall coarse grass species by wildlife grazers (oryx and zebra) and increase nutrient absorption from poor quality forage due to additional microbial fermentation in enlarged portions of lower intestinal tract (Langer 1988). This minimizes competition for palatable grass species between cattle and wildlife. When herbage availability decreases during the dry season, small ungulates move to areas with high density of shrubs, thus minimizing competition between grazers and mixed feeders for palatable grasses (Kuzyk *et al.* 2009).

Although published reports (e.g. Casebeer & Koss 1970; Hoppe *et al.* 1977; Voeten 1999; Voeten & Prins 1999), suggests similarity in preference for same forage plants, thus dietary overlap implying competition between wild herbivores and cattle for forage, the results of bivariate correlation matrix (Tables 11, 12, 13 and 14) indicate that there was no significant correlation (no dietary overlap, p>0.05), which implies variation in diets between cattle and wild herbivores as evidence that grazing by wild herbivores does not affect cattle diet. Furthermore, dietary overlap between livestock and wildlife should not be the only measure of competition among grazing animals since dietary overlap is not constant and forage intake depend on animal preference and environmental influence (Vavra *et al.* 1999).

Wild herbivores consumed only 6 % of the total forage biomass per hectare during the wet and dry seasons compared to more than 16 % of forage biomass consumed per hectare by cattle during the wet and dry seasons (Chapter 4). Cattle consumed almost three times the amount of forage biomass consumed by wildlife. Small (<2kg) dry matter intake by oryx and Grant's gazelle is provide evidence that forage consumed by small wild ungulates may not affect the availability of forage to cattle and the removal of one hartebeest, oryx or Grant's gazelle will each support less than 0.5 livestock units of Boran cattle. Smaller wild ungulates are concentrate selectors and consume smaller quantities of highly digestible forage such as forbs and browse (Wiegmann & Waller 2006; Zimmerman *et al.* 2006) and the presence of small wild ungulates will have little effect on forage availability to the cattle. The results of this study are in contrast with the results by Odadi *et al.* (2011) whose experiment compared cattle weight gain (OMI), organic matter intake, dietary digestible organic matter (DOM), crude protein (CP), DOM/CP ratio and herbage cover in treatment plots accessed exclusively by cattle, and those shared with medium sized wild herbivores, with or without megaherbivores (i.e. 'C', 'WC'and 'MWC' exclosures). The results indicated depressed gain when cattle foraged in areas accessible to wild herbivores during the dry season (evidence of competition). In contrast this pattern was reversed in the wet season with increased cattle weight gain in treatments shared with wild herbivores. The loss in body weight in the dry season was likely to be due to intake of poor quality grass forage (low nutrients). For instance, results on diet (Table 18) show that in dry season crude protein content in cattle diet was low (4.5 %) compared to 6.5 % in the diets of hartebeest and Grant's gazelle (mixed feeders). Conversely in the wet season, the diets of cattle, hartebeest and Grant's gazelle had almost similar crude protein content (7.0 %, 7.25 % and 7.5 %) indicating high quality forage (grasses and forbs) consumed by cattle and wildlife. The high crude protein concentrations in the diets of mixed-feeders could also be associated with the protein-precipitating effect of tannins and not necessarily because high intake palatable of plant species high in protein content (Mbatha and Ward 2006). There is high consumption of forage plants in the wet season when forage quality was high (Odadi 2004) and there is usually an increase in dry matter intake with high crude protein content in the herbage (Payne 1963a). Intensive defoliation of palatable plants frequently reduces plant species diversity (Crawley 1983).The high utilization of *Themeda triandra*, *Lintonia nutans* and *Bothriochloa insculpa* by cattle (Table 6) and high decline of corresponding biomasses (Fig. 9) on Mpala ranch was demonstrated that these grasses were palatable and hence selected. The decline in the composition and biomass due to heavy grazing by cattle resulted in the increase of less palatable and hence less preferred grass species such as *Brachiaria eruciformis*, *Aristida congesta* and *Eragrostis tenuifolia* (Table 2).

Low dietary crude protein contents in herbivores feeding on natural vegetation on Mpala Ranch are evidence of the quality of forage consumed in semi-arid environment. Protein content of grasses in the tropics is very often low (as indicated in Table 19) especially in the dry season and low protein intake could in turn affect intake of energy and other nutrients (Arman *et al.* 1975). These results showing low protein in the diet herbivores grazing on natural vegetation are in contrast with the results by Arman and Hopcraft (1975), which indicated high faecal nitrogen contents from confined animals; eland, hartebeest, Thomson's gazelle, duiker, sheep, boran and friesians fed on pelleted diets containing different amounts of protein. The high dietary mineral content of herbivores during the wet and dry seasons compared to mineral content in the forage was because of mineral licks by the herbivores from the soil on the ranch which contributed to the increase in the mineral content in the diets of herbivores.

Grazing preference for forage plants

Selection of specific forage plants, particularly during the dry season was influenced by forage quality and the nutritional body requirements of the grazing herbivores. For instance, high proportions of coarse tall grasses; *P. mezianum, P. stramineum,* in the diet of zebra and high proportions of forbs and shrubs in the diet of hartebeest and Grant's gazelle during the dry seasons (Tables 8 and 9) is an indication of resource partitioning by wild ungulates. Small ruminants select diet high in nitrogen content (Arman *et al.* 1975) and low in fibre content during the dry season when food quality declines. Grasses with high lignin content during the dry season (Demment & van Soest 1985), are avoided by the small wild ungulates (hartebeest and Grant's gazelle) but consumed by cattle. Mixed-feeders graze on short grasses in the wet season and browse on shrubs with relatively high crude protein in the diet during the dry season (Mason 1969). Diet selection of forage plants by wild herbivores may significantly reduce the potential competition for forage and enhance coexistence of wild herbivores and livestock in rangelands. Moreover, diet selection due to plant species preference, thus resource partitioning enhances divergence in diet among wild herbivores minimizing the potential competition for nutrient-rich forage between wild herbivores and cattle. However, preference and hence high intake of forbs by small wild ungulates (e.g. hartebeest and Grant's gazelle) may lead to reduction of palatable forage plants in the pasture resulting in depressed food intake by cattle affecting livestock production in semi-arid lands. The preference and thus selection of high quality forage by ruminants is to enhance fermentation in the rumen to take place since ruminants are constrained by the minimum protein concentration of 7 – 8% in the diet to make fermentation in the rumen possible (Hofmann 1973; Grant *et al.* 1995).

Therefore, the results indicate herbivores utilizing forage on rangelands have low intake of essential nutrients such as crude protein that may affect intake of digestible dry matter, resulting in low growth rates and decline in livestock production. The results also demonstrate that diet selection and hence high consumption of forbs and shrubs by small wild ungulates may not deprive cattle of palatable grass species which comprise high proportion of cattle diet in wet and dry season in semi-arid lands.

The implications of wildlife grazing together with cattle on forage quality in semi-arid lands

Although high proportions of grass species in the diets of wild herbivores on Mpala Ranch are evidence that wild herbivores may deprive livestock of nutrients in semi-arid lands, grazing intensity and rainfall may have an influence on forage quantity and quality in arid and semi-arid lands. Nevertheless, the multiple use of grasslands by grazing and browsing animals can be highly productive per unit area of land because various animal species utilize variety of vegetation types when forage is abundant (FAO/UNEP 1985). No single herbivore species is likely to make full use of the mixed botanical plant communities that occur throughout the rangelands (Grootenhuis & Prins 2000) and grazing preference on plant species by wildlife and livestock enhances utilization of the high diversity of plant communities on rangeland ecosystems (Gwynne & Bell 1968). Preference for grass or browse enhances the coexistence of grazers and browsers on rangelands (Gwynne & Bell 1968).

Conclusion

Grazing by large wild herbivores may affect cattle diet in the dry season because of an increase in intake of palatable grass species, such as *Themeda triandra*. However, selective feeding by small wildlife during the dry season may reduce competition for forage between small ungulates and cattle through resource partitioning. Small wild ruminants preferred palatable forage plants high in nutrient content that provide the energy required to sustain high body metabolism, whereas high intake of coarse grasses by wild herbivores such as zebra may also minimize competition for other forage plants consumed by cattle. Selective feeding by wildlife defines a distinctive ecological niche within a habitat that reduces competition for forage plants. This information that indicates differential preference for forage plant species is fundamental in the manipulation of various combinations of livestock-wildlife enterprises on communal grazing lands that minimizes competition for forage between livestock and wild herbivores but increases livestock production to improve socio-econiomic status of the pastoral communities.

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CHAPTER SIX

Wildlife grazing with cattle (*Bos indicus* Lichtenstein): competition, facilitation or complementation- Synthesis

Introduction

Pastoralists and ranchers in Kenya assert that grazing by wild herbivores on communal grazing lands and ranches competes for forage resources with livestock affecting cattle performance. Savanna ecosystems have economic and biodiversity values and management of savanna ecosystems is on the assumption that wildlife and livestock compete for forage affecting the diet of cattle (Odadi *et al.* 2011). However, there is no data to provide evidence to support this statement. Therefore, the results by Odadi *et al.* (2011) indicating loss in body weight of cattle in the dry season may not be due to decrease in forage biomass as a result of grazing by wild herbivores. In view of this, this study assessed impact of forage preference and intake by wild herbivores on cattle diet that may impact on cattle performance. The findings of this study (Fig. 11 of Chapter 3) provide no evidence that presence of wild herbivores at low stocking densities on rangelands reduces forage biomass in the wet and dry seasons, however, grazing by cattle resulted in a decrease in forage biomass.

The competitive interactions between cattle and wildlife has been debated by ecologists (e.g. Murray & Illius 1996; Mishra *et al.* 2004; Owen-Smith 2002; Prins 2000) due to complexity in feeding patterns by herbivores, habitat and diet overlap and also resource partitioning. Interaction between herbivores is assumed to be competitive when a shared resource is limited and its use by two or more species results in reduced performance (e.g. survivorship, fecundity, or weight gain). Reduced cattle performance is associated with reduced forage intake and consumption of poor diet (Prins 2000). Competition may arise where species reduce shared food resources to levels below which they cannot be efficiently exploited by other species (Illius & Gordon 1992) and competition is unavoidable if there is overlap in habitat use and the resources are limited (Wiens 1989). Although indicative of potential for competition, overlap in observed patterns of resource use, whether high or low, does not necessarily imply anything about levels of competition in practice (Putman & Putman 1996). A study by Odadi *et al.* (2011) in the same exclosures assessed whether or not wild herbivores compete for food resources with cattle. They hypothesized that if native ungulates compete with cattle, then cattle should experience decreased weight gain associated with decreased forage availability and quality, reduced selection of major herbage species and depressed food intake. The experiment compared cattle weight gain based on organic matter intake (OMI), dietary digestible matter, crude protein, the ratio of DOM/CP and plant species cover in exclosures graze by cattle alone, grazed by catle with medium sized (>15kg) wild herbivores, and cattle grazeing together with large and mega-herbivores (i.e. C, WC and MWC). The results indicated loss in cattle body weight when cattle foraged in areas accessible to wild herbivores during the dry season which is evidence of competition, whereas there was weight gain in exclosures grazed only by cattle. However, the study by Odadi *et al.* (2011) did not examine the proportions of forage plants in cattle and wild herbivore diet to ascertain competitive interaction between cattle and wild herbivores at plant species level and the effect of grazing by wild herbivores on forage biomass resulting in reduced forage availability, thus a knowledge gap still existed. In view of this knowledge gap the purpose of this study was to assess impact of grazing by wildlife on forage biomass and the influence of preference of forage intake by large wild herbivores on cattle diet that may result in decrease in cattle performance (e.g. weight gain). Knowledge of the diet selection by coexisting herbivores is of prime importance in order to make guidelines for livestock management alongside wildlife conservation (Karmiris *et al.* 2011). Coexistence occurs because species with sufficiently high dispersal rates persist in sites not occupied by superior competitors (Butt & Turner 2012). Wildlife comprises mobile individuals that are highly likely to co-exist because of their ability to move and make choices (Richie 2002).

Facilitation, the opposite of competition is defined as a form of beneficial interaction between herbivores, whereby food material is made available by the activities of another (Sinclair and Norton-Griffiths 1982, Letham 1999). Facilitation is deduced to occur if one species enhances performance of another species through improved food quality or intake via modification of the habitat (Arsenault & Owen-Smith 2002). Facilitation has been observed in open grasslands, mostly in African savannah (Sinclair & Norton-Griffiths 1982, Augustine *et al.* 2010) which indicates beneficial interactions between livestock and wild herbivores. Livestock has beneficial effects on wild ungulates through the redistribution of soil nutrients because native ungulates selectively used glades (bomas or temporary corrals) relative to surrounding nutrient poor habitats (Augustine *et al.* 2010).

Complementary feeding is exhibited by large mammalian herbivores using forage resources that will rarely if ever be used by other mammalian herbivores. The most striking example is the elephant, although it feeds on grasses and leaves of trees and shrubs, it consumes branches and bark and thus enhancing the herbaceous layer. Thus, specialist browsers like elephants are complementary to livestock in their use of their primary resources (Gordon *et al.* 2008). Exclosures in which elephants and giraffe browsed on trees and shrubs indicated an increase in cover of grasses in exclosures in which elephant and giraffe were allowed (Riginos & Young 2007). Intensive browsing by mega-herbivores (elephant and giraffe) opens up dense shrubland and thus facilitates the germination and growth and increases the abundance and forage production of herbaceous plants (Cesar *et al.* 1996; du Toit 1998). Preferential feeding by wild herbivores may increase plant diversity in a pasture (Hughes 1993; Nolan *et al.* 1993; Bailey *et al.* 1998).

Evidence

This study examined the response of forage biomass on grazing by large wild herbivores and cattle and the results indicate that cattle consumed an average of 8 % of the total forage biomass available in the exclosures in the wet and dry seasons, whereas wild herbivores consumed an average of 6 % in the exclosures grazed only by wildlife in the wet and dry seasons. However, the introduction of cattle in the exclosures grazed by wild herbivores consumed 12 % of total forage biomass available in the pasture (Fig. 12 of Chapter 4). The results of this study show that the difference in forage biomass consumed between cattle and cattle grazing together with wildlife was small (42 kg ha^{-1}) which demonstrates that grazing by wild herbivores has little effect on forage biomass and hence loss of body weight of cattle may not have been caused by inadequate forage biomass available in the pasture due to grazing by wild herbivores. The loss in body weight in the dry season was likely to be due to intake of poor quality forage (low nutrients) by cattle since the forage was dry with low nutrient content. This argument is supported by low (4.5 %) CP in cattle faecal content in the dry season compared to that of hartebeest and Grant's gazelle with high (6.5 %) CP content (mixed feeders) (Table 18 of Chapter 5) which indicates that the smaller wildlife selected nutritious forage. Conversely in the wet season, the diets of cattle, hartebeest and Grant's gazelle had similar crude protein content (7.0 %, 7.25 % and 7.5 %) an indication of high crude protein content in the forage consumed.

There are low levels of utilization and there is high accumulation of residual grass biomass (>900 Kg/ha) in exclosures exclusively grazed by wildlife compared with high utilization and low accumulation of residual forage biomass (<250 kgs/ha) in exclosures grazed by cattle (Fig. 9 of Chapter 3). The low level of forage utilization by wildlife and hence high accumulation of residual biomass provides evidence that low stocking density of wild herbivores does not cause high reduction in forage biomass. Therefore, the small difference in forage biomass between exclosures grazed by cattle with wildlife and cattle alone, and high accumulation of residual forage biomass in exclosures grazed by wild herbivores does not support the hypothesis that grazing by wildlife results in decline of forage biomass.

There were variations in the proportions of dominant grass species (*Brachiaria lachnantha*, *Pennisetum stramineum*, *P. mezianum*, *Themeda triandra*, *Lintonia nutans* and *Bothriochloa insculpta*) species between the diets of cattle and wild herbivores. However, there was low significant difference (r= 0.345*, p<0.038) in proportions of dominant grass species in the diet of cattle and zebra and highly significant differences (r= 0.928**, p<0.007; r= 0.869*, p<0.001) in proportions in the diet between cattle and hartebeest and between diets of cattle and Grant's gazelle in the dry season. The results imply high overlap in the diets of cattle and zebra, thus competition for grass forage between cattle and zebra (grazers with similar body size) and no competition for grass forage between cattle and small wild ungulates (mixed feeders). Likewise the results on dry matter intake also indicate a small (<1kg) difference in dry matter intake by cattle and zebra and large (>1kg) difference in dry matter intake between cattle, hartebeest and Grant's gazelle (Tables 12 and 13 of Chapter 5). However, the similarity in dietary crude protein content (7 %) in the diets of cattle, hartebeest and Grant's gazelle indicate preference for high quality forage was probably due to the abundance of nutritious forage plants in the pasture during the wet season. Therefore, the overlap in proportions of forage plants in cattle and zebra diets and similarity in the crude protein content in the diets of cattle and small ungulates during the wet season support the hypothesis that grazing by large wildlife has an effect on the diet of cattle.

The facilitative effect was shown by a strong correlation between cattle grazing and plant species richness and species turn-over (Fig. 5 and 6) which implies that cattle grazing increases plant species diversity that may enhance diet selection among grazing wild herbivores minimizing competition for forage plants between cattle and wildlife. A facilitative effect was also shown by an increase of 2 – 10 % in less dominant short grass species (*Eragrostic tenuifolia, Sporobolus festivus* and *Dinebra retroflexa*) (Table 2 of Chapter 2) in the exclosures grazed by cattle which may be utilized by the small ungulates minimizing competition on *Themeda triandra* and *Lintonia nutans* (tall nutritious grasses).

Complementary feeding was demonstrated by resource partitioning, particularly by hartebeest and Grant's gazelle (mixed feeders) which browsed on trees and shrubs in the dry season with less than 50 % grass, >15 % forbs, >13 % shrubs and >10 % trees in the diets , whereas in the wet season the diet comprised >60 % grass, <15 % forbs, <8 % shrubs and <4 % trees (Fig. 8 of Chapter 3). Conversely, the diets of cattle, oryx and zebra comprised mainly grasses with over 75 % in the diet. The preferential selection of forage plants in the pasture during the dry season as exhibited by small wild ungulates and cattle in this experiment is a complementary use of forage resources in the semi-arid lands that enhance co-existence between the grazers and mixed feeders during periods of scarcity.

Discussion

The 52 kg and 188 kg per hectare increment in forage biomass in exclosures grazed by cattle with mega-wildlife (MWC) in the 2008 dry and 2008 wet seasons (Table 7 of Chapter 4) in spite of high stocking rates in the exclosures indicates that browsing by mega-herbivores benefits livestock in terms of habitat modification by reducing tree canopy and thereby enhancing germination of herbaceous plants. The results are consistent with the results by Augustine *et al.* (2010) in exclosures which indicated that native browsers suppress shrub encroachment and enhance forage production. High forage consumption as a result of cumulative effect of cattle grazing with wildlife may result in the decrease in forage biomass on grazing lands. However, the small difference in forage biomass between the exclosures grazed by cattle and cattle grazing with wildlife in the dry season imply that there was no scarcity of forage thus the loss of body weight of cattle was not due to decline in forage quantity. Grazing during the dry season leads to greater energy expenditure by cattle through less efficient selective grazing or longer movements to grazing patches (Ayantunde *et al.* 1999). Competitive interactions between cattle and wildlife are expected to be higher during the dry season as the energy balance of grazing animals becomes more limited due to grazing on available forage, which is of poor quality (Butt & Turner 2012). There was no evidence that there was a limitation in the availability of herbaceous forage plants for cattle. The loss in body weight in the dry season was due to intake of poor quality forage by cattle with is (4.5 %) crude protein and high crude fibre contents in the diet compared to high (7.0 %) crude protein content in the diet in the wet season and 7.25 % and 7.5 % faecal CP content of hartebeest and Grant's gazelle. Low faecal crude protein content in cattle was likely due to preference and hence competition for scarce palatable grasses between cattle and wildlife leading to ingestion of low quality forage by cattle. Dry-season grazing simply reduces the stock of dry fodder available causing higher-quality forage to become less available during the same season (Butt & Turner 2012). Animal performance of grazing herbivores reflects forage quality of a pasture (Newman *et al.* 2010). In the dry season lignin content in the grasses increases and there is a decline in crude protein, thus leading to diet selection by small wild ungulates feeding on forbs and leaves of shrubs and trees with high nutritive value whereas cattle feed mainly on grasses of low quality. Herbivores graze selectively and the selection is determined by preference associated with quality and taste (Baumont 1996). The small wild ungulates respond to variability in forage quality by selecting forage plants which are non-stemmy and accessible leaves of high nutrient content given their greater energy requirement (O' Reagain 1993). However, preferential feeding by wild herbivores may increase plant species diversity in a pasture (Hughes 1993; Nolan *et al.* 1993; Bailey *et al.* 1998). Furthermore, intensive browsing by mega-herbivores (elephant and giraffe) opens up dense shrubland and thus facilitates the germination and growth and increases the abundance and forage production of herbaceous plants (Cesar *et al.* 1996; du Toit 1998). Over an evolutionary time scale, natural selection promotes clear separation in resource use by various herbivores specifically to minimize the loss of fitness incurred through competition (Putman & Putman 1996).

That small wild ungulates consumed high proportions of shrubs and forbs (high quality food items, Table 9) is comparable with results by Ferrer Cazcarra and Petit (1995) on young and adult cattle. The results indicated that calves had high energy requirements relative to their body size and were shown to select higher quality food items. Similarly the results are comparable with those of Ferruggia *et al.* (2006) that lactating cows with high energy requirements for maintenance and lactation consumed a greater proportion of their bites from green patches than did dry cows. However, the high consumption of forbs by small ungulates is unlikely to have a significant effect on the diet of cattle because cattle feed mainly on tall palatable grasses (Table 8).

Recommendations for further research

The various techniques used to assess the effect of wildlife and cattle forage utilization on forage biomass and dietary nutrient content between wild herbivores and cattle confirmed that determination of competitive interaction between livestock and wild herbivores on forage resources on rangelands is complex. Further investigation needs to be carried out on competitive interactions between wild herbivores and cattle by comparing live-weight of cattle grazing together with wild herbivores on communal grazing lands alongside measurements of forage biomass to determine the effect of seasonal changes of forage biomass on cattle performance. The measurements of live-weight of cattle should be taken at fixed time intervals in the wet and dry seasons. The study will provide reliable data that show the actual effect of sharing of forage between wildlife and cattle on communal grazing lands.

Although this study determined the effects of grazing by wildlife and cattle on plant composition, forage utilization and residual forage biomass in controlled plots on a cattle ranch, there are no data available on forage utilization and forage biomass. The information will enhance forage resource evaluation and monitoring on communal grazing lands, thus there is a need for a study to be conducted to provide data on the trend of forage biomass due to sharing of forage resources between livestock and wildlife on communal grazing lands. Monitoring and evaluation of forage biomass will provide useful information that is important in making decisions and recommendations by the relevant Government Ministries and Non-government Organizations in maintaining livestock and wildlife numbers that is consistent with forage biomass without compromising quality of livestock products on communal grazing lands. Therefore, forage utilization and forage biomass on communal grazing should be measured by establishing a pasture monitoring programme to determine the relationships between cattle performance (live-weight of cattle) and available forage biomass. Monitoring points should be established on each grazing area with fifty (50) 1m^2 cages with wire mesh placed permanently along 4 transect lines laid in opposite directions from the centre of a grazing area/block and plant species at each monitoring site identified inside the cage and on open grazing areas and recorded before forage biomass measurement is taken. This is because some plant species serve as indicators of range condition and trend. Monitoring should be done during the wet and dry seasons each year to assess changes in forage biomass. Forage utilization provides important information on intensity of grazing, which provides a basis for formulating grazing management plans and adjustment of stocking rates on the communal grazing lands. Utilization measurements at the end of the wet season may provide information on pasture condition thus reduction of stocks or other management changes that are required before degradation of vegetation occurs

(Smith *et al.* 2007). Sustainable forage utilization on communal grazing lands can be achieved by maintaining low stocking rates reducing grazing pressure on forage resources and enhance incorporation of wildlife in pastoral livestock production systems, thus leading to diversification of forage resources.

Conclusion

Competitive interactions between cattle and wild ungulates are dependent on body size of wild herbivores and forage quality, whereas facilitative and complementary interactions between wildlife and livestock are influenced by forage preference and feeding patterns of cattle and wild herbivores. The potential for competition for palatable herbaceous forage plants between livestock and small wild ungulates on communal grazing lands cannot be ignored, particularly with increases in livestock and wildlife numbers on communal grazing lands (Ottichillo 2000a). If competition is ignored and each herbivore species is stocked at its independent 'carrying capacity, resource overuse and diminished animal performance could result. If stocking is restricted to distinct food and habitat preferences, benefits of facilitation and fine-scale resource partitioning are enhanced (Owen-Smith 2002).

Knowledge on forage preference and diet selection between cattle and wild herbivores is important in the understanding of livestock-wildlife interactions in order to enhance livestock production without compromising wildlife conservation in semi-arid lands in Kenya. The presence and browsing of mega-wildlife opens up the canopy cover of trees and shrubs and increases forage biomass that could support larger numbers of livestock with minimum rangeland degradation. Therefore, it is important for pastoralists to optimize on livestock numbers on high forage bimass and quality in wet season and reduce the cattle herds during the dry season to utilize the scarce palatable forage plants available without compromising the body condition of cattle. The findings of this study will also form a basis for policy formulation on rangeland resource monitoring and evaluation and human-wildlife conflict resolution strategies and improvement of socio-economic welfare of the pastoral communities and economic development of the country.

The major contribution of this study is that cattle lost condition (Odadi *et al.* 2011) not because of decrease in standing biomass in the pasture but because of poor quality graze (i.e. low crude protein content) during the dry season.

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