

**EFFECTS OF VEGETATION BURNING ON THE FORAGING STRATEGY OF
WATERBUCK, WILDEBEEST AND REEDBUCK IN A MOIST SAVANNA OF
TANZANIA**

BY

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ABSTRACT

Savannah grasslands are occupied by large mammal herbivores whose ecological separation between and within each guild have resulted to different foraging strategies and preference for forage differing in attributes to reduce competition between them. Therefore, the current study aimed at: 1) measuring the relative use of burnt and non-burnt areas by waterbuck, wildebeest and reedbuck, and their possible shifts between the two patches over time; 2) assessing forage characteristics in grazed sites on burnt and non-burnt sites along with the post fire nutritive quality of the grasses; and 3) testing the notion that waterbuck is an intermediate grazer between wildebeest, a bulk grazer and Bohor reedbuck, a selective grazer. The study was conducted during dry season in Saadan National Park, a moist, tall-grass savanna. The animals were found not equally distributed between the two grassland patches, with most occupying burned areas. On the other hand, previously grazed patches were actively selected for feeding, and Nitrogen content of the main forage grass species was high in grass samples collected 80 days since fire. Contrary, NDF and ADF concentrations were very low in grass samples collected 80 days post fire but increased after six months. Reedbuck had the shortest bout lengths for all behaviours whereas waterbuck showed the longest bout sessions. Reedbuck grazed at taller grass height than waterbuck and wildebeest grazed the shortest grassland patches. Wildebeest grazed mainly on *Panicum infestum* despite of its greenness status while the waterbuck and reedbuck grazed mostly on green materials. The non-random patterns in animal's distribution between burnt and non-burnt grassland patches suggests that fire is an important adaptive management strategy for Saadani National Park.

DECLARATION

I, CECILIA MARTIN LEWERI, do hereby declare to the Senate of Sokoine University of Agriculture that this dissertation is my own original work and that it has neither been submitted nor being concurrently submitted for degree award in any other institution.

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DEDICATION

This work is dedicated to my parents; Martin Francis Leweri and Judith Hubert Shio, they tuned my youth in favour of education. Also to my young brother and sister Frank and Mary that they may be inspired to get highest levels of education in their life time.

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LIST OF ABBREVIATIONS

ADF	Acid Detergent Fibre
ANOVA	Analysis of Variance
GPS	Global Positioning System
IUCN	International Union for Conservation of Nature
N	Nitrogen
NDF	Neutral Detergent Fibre
P	Phosphorus
SANAPA	Saadani National Park

CHAPTER ONE

1.0 INTRODUCTION

1.1 Background Information

African savannah extend in a broad semicircle running from West to East Africa sandwiched between rain forest and desert, characterized by a continuous grass layer interspersed with trees under a climatic regime of distinct wet and dry seasons (Du Toit and Cumming, 1999; Shorrocks, 2007). The dynamics of woody and herbaceous vegetation are mainly driven by soil moisture, fire, nutrient availability and mammalian herbivory (Bond 2005; Sankaran *et al.*, 2005; Holdo *et al.*, 2009). A distinction can be made in the vast majority of African savannah between the humid/moist dystrophic savannah which is also referred to as mesic savannah, and dry/arid eutrophic savannah, with the latter being relatively nutrient rich (Bell and Koch, 1980; Huntley, 1982; Du Toit and Cumming, 1999). Humid savannah of Africa are the most frequently burnt ecosystems in the world with fire frequencies of up to twice a year in some places and about half of its total surface being estimated to burn at least once in every year (Bond and Keeley, 2005; Hao, 1994). These areas are fire prone due to its high productivity and therefore large fuel loads (Cech, 2008). Fire is therefore playing a great role in maintaining the balance between the woody, grass cover and productivity in this type of savannah whereas in the drier savannas this balance is mainly determined by water availability (Aranibar *et al.*, 2004; Sankaran *et al.*, 2005).

African savannah grasslands are a heterogeneous forage resource that exhibit strong temporal and spatial dynamics of forage quality in terms of protein content and digestibility (Drescher *et al.*, 2006). These characteristics have made the African Savannah to be primarily occupied by herbivores many of which eat grasses either as grazers or

mixed feeders (Shorrocks, 2007). The African savannah herbivore comprises about 46 extant ungulate species (Woolnough and Du Toit, 2001) divided into two major distinct feeding guilds i.e. grazers, which feed primarily on grasses and forbs, and browsers, which feed primarily on leaves of woody vegetation (Holdo *et al.*, 2009). The important ecological separation between and within each guild is their difference in body size and secondarily through adaptations in the digestive system (Woolnough and Du Toit, 2001). This distinction has therefore led to differential preferences for grass height and forage quality and hence reduced competition among them (Illius and Gordon, 1987; Owen-Smith, 1989; Prins and Olf, 1998; Arsenault and Owen-Smith, 2002).

In African savannah communities specifically with tall grasses, grazing animals with narrow, pointed muzzles are more capable of selecting leaves compared to ones with relatively broad muzzles (Ego *et al.*, 2003). The Bohor reedbuck (*Redunca redunca*) for example, a medium sized grazer which tends to graze plant species selectively from plant communities (Jungius, 1971), would be at an advantage in this environment. The relatively broad muzzles of wildebeest (*Connochaetes taurinus*) and other bulk grazers could restrict the degree of selectivity possible in this habitat (Ego *et al.*, 2003). On the other hand, the common waterbuck (*Kobus ellipsiprymnus*) that is considered to be an intermediate grazer, eating both medium height grasses and short grasses (Spinage, 1982) would benefit from the grazing impacts of these larger species, and potentially outcompete them when food supplies become reduced (Murray and Illius, 2000). Hence, the influence of oral morphology and dentition on feeding confirms the advantages of species with broad muzzles on short grasslands as compared to tall grasslands (Murray and Brown, 1993).

Moreover, bulk feeding ungulates with low selectivity could also be able to maintain a high quality food by concentrating their feeding on certain habitat types (Ben Shahr, 1991) or on particularly nutrient rich grassland patches, as for example recently burned areas with regrowth or self-created grazing lawns (Jarman, 1974; McNaughton, 1984; Fryxell, 1991; Tomor and Owen-Smith, 2002; Archibald and Bond, 2004 ; Grant and Scholes, 2006).

Variation grass height and bulk density, i.e. the amount of forage available per unit volume, on the other hand also affects the selective feeding behaviour of grazing ruminants (Hassan *et al.*, 2007) through its effect on forage availability and quality and hence diet of grazing ruminants (Murray and Brown, 1993). It influences ingestive behaviour of the grazing animal as well as bite weight which in turn affects daily intake and hence animal performance as a whole (Gong *et al.*, 1996).

In the humid/dystrophic African savannah, forage maturation is more pronounced due to its high rainfall (Verweij *et al.*, 2006), causing a gradual decrease in the nutritive value and digestibility of the forage (McNaughton, 1979; Verweij *et al.*, 2006). The effect of this is expected to be a spatial pattern of consumption by grazers so as to balance the trade-off between intake rates and forage nutrition quality (Fryxell *et al.*, 2004). Following this, selection of grass is therefore influenced additionally by the effective mouth width relative to body size, as this will be controlling the bite mass and hence rate of food ingestion to achieve their daily intake, especially on grass swards differing in structure (Gordon and Illius, 1988). Besides nutritive food requirements, habitat choice of an animal also depends on several other factors such as: water availability, predator avoidance and interaction with other wildlife species (Redfern, 2003; Sinclair, 1985). Predator avoidance may be difficult in dense bush for open plain species like wildebeest which rely on

predator detection in open areas with good sighting distance (Lamprey 1963; Estes, 1991). For other species the grass height may be especially important (Traill, 2004), Bohor reedbuck for example rely on tall grass to lie down and hide in case of danger (Estes, 1991; Jarman, 1974).

1.2 Problem Statement and Justification

The Saaadani ecosystem includes a newly formed National Park (Saadani National Park), which comprises areas that have gone through different land uses; an agricultural area to a game reserve (Saadani North), a cattle ranch to a game reserve (Mkwaja North); and now a National Park. Conversion of an area with natural animal and vegetation communities to an agricultural land or to a cattle ranch with depleted communities and back to natural animal communities may have significant influences on vegetation structure and hence, effects on ecosystem structure and function. Such a unique history has provided a mosaic-like landscape offering experimental opportunities to investigate feeding of ungulate species under various habitat conditions.

Early dry season burning is considered to be an important management tool in the Saadani National Park (SANAPA) with the intention to create open areas of green flush of elevated nutrient quality and to maintain the openness (Anderson *et al.*, 2007). Some uncontrolled burning by poachers or accidental fires also occurs towards the late dry season but basically has the same effect. Burning also causes spatial differences in grass species composition, structure and condition (greenness), and nutritional quality (van de Vijver *et al.*, 1999). Nevertheless, burning in SANAPA is carried out without clear knowledge on its influence on grazing patterns of ungulates between burnt and non-burnt patches and possible shift between them. It is therefore important to study how these grazers utilizes forage resources in the two strata (burnt and non burnt patches).

Reedbuck are able to graze in heterogeneous tall grass vegetation by selecting single (short) plants or tufts (Jungius, 1971) whereas wildebeest depend on homogenous patches of at least several square metres (grazing lawns) which comprised of short and nutritive grass (McNaughton, 1976). Moreover, the waterbuck regularly graze with wildebeest on non-burnt areas (a persisting situation throughout the year), this led to an assumption that the present abundance of waterbuck in SANAPA has been boosted by human influence i.e. introduction of wildebeest and fire regime as both fire and bulk grazer can create favourable grazing conditions of palatable and high nutritive quality forage (Augustine and McNaughton 1998; Anderson *et al.*, 2007). The study on the pasture characteristics of the grazing site is therefore important to see their relevance to feeding behaviour of the respective herbivores.

Furthermore, SANAPA contains expanses of moist tall-grass savannah together with a good population of reedbuck and waterbuck which are native and the wildebeest which were introduced from Serengeti National Park. Reedbuck is a selective feeder, which would be expected to pick out the nutrient richest plant species and plant parts while wildebeest (a well-studied ruminant herbivore in semi-arid savannas) is an example of a large bulk feeder, which would be expected to feed on large quantities of average quality food and Waterbuck has been reported to be a selective feeder to some degree (feed intermediate between the bulk and selective grazer) (Tomlinson, 1980; East, 1984; Melton, 1987), although its body mass could indicate a tendency towards a bulk feeding strategy. This study therefore aimed to assess the foraging strategy of the three herbivores and to test the notion that waterbuck shows intermediate of bout lengths between the wildebeest and reedbuck.

This study is set in a larger framework of research on savannah dynamics in Saadani NP started in 2002, with focus on the relationship between grazing and burning effects through experimentation. It is designed to improve our understanding on the effect of burning on grazing of waterbuck, wildebeest and reedbuck on the area. In addition the study will enhance the understanding of what patches (burnt vs non-burnt) are used and why such patches are being used by the three grazers in a particular way. Moreover, the results of this study are expected to serve as a basis on advising the park management on the present fire regime (frequency of burning and spatial differences).

1.3 Objectives of the Study

1.3.1 Overall objective

To study the effects of vegetation burning on foraging strategy of the waterbuck, wildebeest and reedbuck with respect to grass species composition, sward structure, height and nutritional quality of the grasses.

1.3.2 Specific objectives

The specific objectives of the study are:

- i. To study the use of burnt and non-burnt patches by waterbuck and compare it with existing data from Bohor reedbuck and wildebeest in SANAPA.
- ii. To study the pasture characteristics (grass species composition, grass cover and height) and nutritional quality (digestibility as indicated by fibre and protein contents) in burnt and non-burnt patches in relation to grazing.
- iii. To study foraging strategy of waterbuck by means of recording small scale movements on non-burnt patches and compare them with existing data of wildebeest and Bohor reedbuck.

1.4 Hypotheses

- i. Burned areas are preferred by waterbuck to non-burnt with short grassland (grazing lawns).
- ii. The preference of burnt areas is normally distributed (bell-shaped) over time, and is stronger in waterbuck than in reedbuck.
- iii. Preference for sprouts after burning is associated with higher nutritive value of swards after burning.
- iv. Foraging strategy of waterbuck shows a pattern that is intermediate between wildebeest and reedbuck.

CHAPTER TWO

2.0 LITERATURE REVIEW

2.1 Status and Distribution of study animals

Distribution of common waterbuck (*Kobus ellipsiprymnus*) ranges from East of the eastern Rift Valley, southwards it extends to about the Hluhluwe-Umfolozi National Park in KwaZulu-Natal, and to central Namibia also to the western and northern plateaux of Zambia. It is also found in Democratic Republic of Congo, Uganda, Rwanda, Tanzania, coastal rangelands of Kenya, and from Eritrea and West Ethiopia in a narrow band to Senegal and Mali in West Africa (Skinner and Chimimba, 2005; IUCN, 2009). In Tanzania, good populations of common waterbuck occurs in Tarangire, Saadani and Selous Ecosystems whereas that of defassa waterbuck (*Kobus ellipsiprymnus defassa*) occurs in Serengeti, Moyowosi-Kigosi, Ugalla River and Katavi-Rukwa but about half of these populations are in decline because of poaching (East, 1999). Currently it is listed as Least Concern under the IUCN red list of threatened species (IUCN, 2009). In African savannah ecosystems for example, mortality of this species is often induced by food shortage and by a significant decrease in food quality, and such mortality can even exceed the deaths caused by the various predators (Kassa *et al.*, 2007).

Wildebeest (*Connochaetes taurinus*) are distributed from southern Kenya southwards to northern and eastern Namibia and South Africa to Mozambique north of the Orange River, and from Mozambique to Zambia south of the Zambezi River, and from south-west Zambia to south-east and southern Angola (Estes, 1991). The species is listed as Least Concern as the species overall is widespread and numerous, and present in many protected areas throughout its range. However, its continual existence remains entirely dependent on management regimes, particularly the migratory wildebeest population of the Serengeti-

Mara ecosystem, which accounts for some 70% of total population numbers (IUCN, 2009).

According to the Estes (1991) bohor reedbuck (*Redunca redunca*) is mostly found in Benin, Burkina Faso, Burundi, Cameroon, Central African Republic, Chad, Republic of the Congo, Democratic Republic of the Congo, Ethiopia, Gambia, Ghana, Guinea, Guinea-Bissau, Kenya, Mali, Mauritania, Niger, Nigeria, Rwanda, Senegal, Sudan, Tanzania and Togo. Although bohor reedbuck is a common and widely distributed species and has least concern it still faces the threat of habitat loss and degradation due to too many human settlements into its habitat (particularly in West Africa where reedbuck is scarce), droughts and poaching (IUCN, 2009).

2.2 Species Habitat Preference

Waterbuck (*Kobus ellipsiprymnus*) occurs in those parts of Africa where high rainfall results in tall grasslands (Spinage, 1982), and such grasslands are continuously changing due to rainfall, fire, and herbivory (Deutsch and Murray, 2001). Preferred habitat is mainly open areas of grassy savannah plains with woodland cover or scattered bush clumps as well as reed beds in the riverine areas of both coastal and inland regions (Skinner and Chimimba, 2005). A study in Tarangire National Park by Lamprey (1963) in Spinage (1982) reported waterbuck being selective in its requirement with a strong preference for medium density *Acacia drepanolobium* woodland, but proximity to water being the main determining factor. A study done in a drier part, Mkomazi National Park, also supported this concept of selectivity (Harns, 1972; Spinage, 1982). Despite its name, which has some affinity for the presence of water, waterbuck is not an aquatically inclined species although generally it needs more water than other bovids (Spinage, 1982). In general, waterbuck

prefer dry ground, but they occasionally jump into water or floodplains after they have dried out or to shelter themselves from predators (Spinage, 1982).

The wildebeest (*Connochaetes taurinus*) is a large antelope adapted to relatively dry savannas where shade is provided in the form of umbrella acacias and assemblage of trees and bushes (East, 1984; Kingdon, 1997; Bothma *et al.*, 2002). Wildebeest are social and live in large permanent herds which show migratory behaviour from one feeding ground to the next (Wilmshurst *et al.*, 1999; Traill, 2004). The Bohor reedbuck (*Redunca redunca*) is a medium-sized antelope, which shelters in tall grass (Kingdon, 1997). Reedbucks are adapted to grasslands that change in height and quality of the food supply and survive better than many other herbivorous ungulates in poor grassland (Jungius, 1971).



Plate 1: Waterbuck (*Kobus ellipsiprymnus*)



Plate 2: Wildebeest (*Connochaetes taurinus*)



Plate 3: Bohor reedbuck (*Redunca redunca*)

2.3 Food and Feeding Preference

Waterbuck has been termed a pronounced roughage eater but generally eats the species that are abundant in the area (Skinner and Chimimba, 2005), preferring short to medium sward height (higher than 120 mm above the ground) for grazing and avoiding overgrazed areas (Rohrer, 2007). Most of the species that are positively selected have relatively high protein content as well as high levels of digestible cellulose (i.e., energy content) (Kassa *et al.*, 2007). Waterbuck is considered to have higher requirements of protein than comparable bovids (i.e. about four times more protein in their diet than the other bovids (Taylor *et al.*, 1969), apparently in accord of their high water intake and the consequently high urine output (Spinage, 1982). Occasionally waterbuck may feed by browsing for up to almost 21% of its feeding time so as to balance protein deficiency in the graze (Spinage, 1982) as there is a higher protein/fiber ratio in browse compared to grass and hence higher nutritive value (Codron *et al.*, 2007). However, browsing behaviour is considered to be more common in the night compared to day time (Spinage, 1982).

Wildebeest are concentrate bulk feeders and prefer short (not taller than 150 mm), lawn-like grasslands with rapid regrowth and shows migratory behaviour from one feeding ground to the next (Estes, 1991; Wilmshurst *et al.*, 1999; Bothma *et al.*, 2002; Traill 2004). Reedbuck are selective grazers but in the dry season they often include dicotyledonous browse in their diet as these contain more protein and less fiber than grass leaves (Lamprey, 1963; Gutbrodt, 2006; Owen Smith, 1982). The reedbuck tend to be nocturnal when food and water are abundant but in the dry season, when these resources become limited, it becomes more diurnal (Jungius, 1971; Kingdon, 1997; Bothma *et al.*, 2002). Females generally group in home ranges during the wet season when most young are born and males tend to be scattered in the area. During the dry season females search the best remaining grazing areas and male reedbucks compete for the females, which possibly

results in submissive males having to feed in inferior grazing areas (Kingdon 1997). Fires and drought drive the reedbucks into temporary larger groupings of up to 20 animals (Kingdon, 1997; Bothma, 2002).

2.4 Effect of Fire and Grazing on Forage Structure and Quality

Herbivory and fire are the two major influencing factors that drive tree-grass dynamics in African savannas (Hagenah *et al.*, 2009). They consume vegetation and act as top-down controllers on savanna structure and condition (Bond, 2008).

Herbivores influence biomass and species composition of fodder grasses (Du Toit and Cumming, 1999; Treydte *et al.*, 2009) by preventing prevalence of older, lignified tissues and stimulate the growth of younger, less lignified leaves (Anderson *et al.*, 2007). This also increases light intensity to the underlying tissue as well as changing the hormonal distribution by the removal of apical dominance (Atsuchi and Norio, 2004), in which with repetition induce changes in leaf tissue chemistry of re-growing tissue (Anderson *et al.*, 2007). Similarly, they recycle limited nutrient (De Mazancourt *et al.*, 1999) by increasing N and P contents of soil through deposition of dung and urine in the feeding areas, which in turn triggers enhanced productivity and fresh re-growth of the grass materials (Du Toit and Cumming, 1999; Treydte *et al.*, 2009).

Fire on the other hand reduces aboveground biomass by removing dead/old tissue (Anderson *et al.*, 2007). Removal of accumulated biomass can stimulate regrowth, producing young plant material that is more digestible and nutritious than older tissue and hence offers improved forage quality (Verweij *et al.*, 2006), because the concentration of nitrogen in live leaves is enhanced (Prins and Beekman, 1989; Verweij *et al.*, 2006). Fire also alleviates nutrient poverty by making the nutrients stored in the fuel available to

plants (Orians and Milewski, 2007). This causes the post fire re-growth to be superior forage in terms of quality and sward structure, hence attract many grazing herbivores (Klop and Prins, 2008). However, fire might have different effects between selective and bulk grazers, as these have different needs concerning quality and quantity of food (Wilsey, 1996). If the burned areas are quite limited in size, those areas might be transformed to grazing lawns, whereas large-scale fires might even dilute the effect of grazing lawns (Archibald, 2005).

CHAPTER THREE

3.0 MATERIAL AND METHODS

3.1 Study Area Description

Saadani National Park (SANAPA-680 km²) is located on the coast of Tanzania (5° 43' S, 38° 47' E), approximately 160 km north of Dar es Salaam (Fig. 1). Specifically, the study was carried out in the area known as Saadani North (110 km²), which formerly used for agriculture, mainly sisal plantations, and was transformed into a game reserve in 1969 (Gutbrodt, 2006). The rainfall in SANAPA is bimodal consisting of a short rainy season from October to December during which monthly averages exceed 100 mm, and a long rainy season from March to the beginning of June (Tobler, 2001; Bloesch and Klötzli, 2002). The dry months are January, February, July, August and September (Cech, 2008). Due to rainfall of around 900 mm and due to the nutrient poor soils (Cech, 2008), this savannah can be classified to be humid dystrophic (Huntley, 1982; Tobler *et al.*, 2003). Humidity is relatively high throughout the year; thus there are no months which are absolutely dry and even the dry ones are not so severe (Bloesch and Klötzli, 2002). Mean annual temperature is 26°C with an annual range of 5°C and a daily range of 8°C (Bloesch and Klötzli, 2002).

Soil is relatively nutrient poor consisting of greyish, fine or loamy sand in the flat areas and reddish, loamy sand on ridges of escarpment and hilltops (Cech, 2008). The lowest lying basins along the coast contain saline clay soil (Blosch and Klötzli, 2002). The vegetation of Saadani North is a mesic savannah, but the variability of both the grass and tree components produce a large scale mosaic of rather different habitats such as open grassland plains, palm and acacia-dominated savannah, open acacia woodland, patches of evergreen bush, and riverine forest strips (Gutbrodt, 2006).

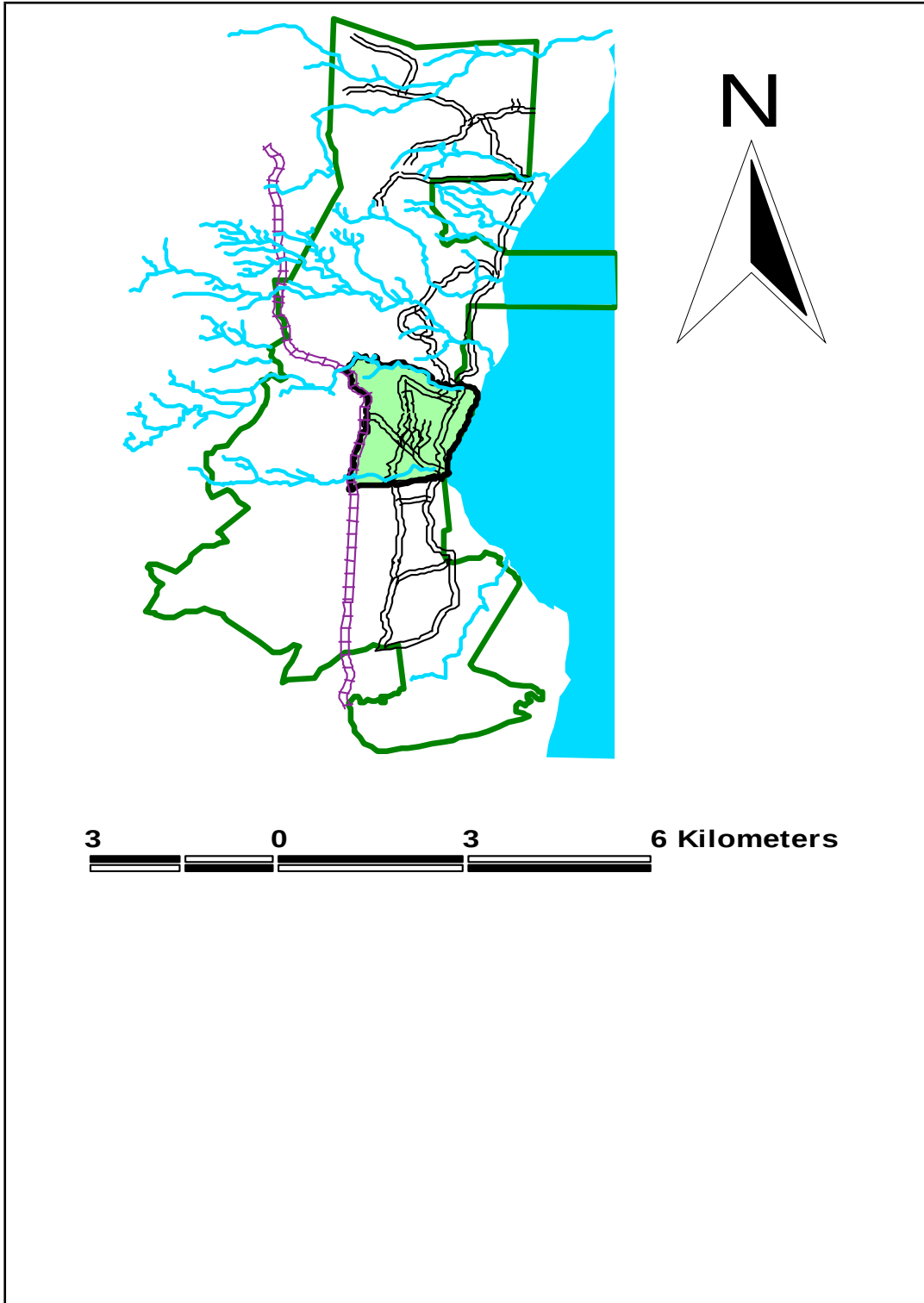


Figure 1: Map of Saadani National Park, Tanzania

Source: Gutbrodt, (2006).

3.2 Study Design

The study measured the relative use of burned and non-burned areas by waterbuck compared to wildebeest and reedbuck, and possible animal shifts between the two patches over time. This was done along standardized road drives (the same roads) by mapping animals along a strip on both sides of the road by means of a GPS (Fig. 2). To assess characteristics of grazed sites on both burned and non-burned sites in which 20 observations (replicates) were done for each animal species. Data on the nutritive quality of grasses as modified by burning were also gathered from an experimental setup in the same area where 8 plots were subjected to 5 different treatments (burning, mowing, mowing and fertilize with ashes, fertilize with ashes and control). Finally, to test the notion that waterbuck is an intermediate grazer between wildebeest, a bulk grazer and Bohor reedbuck, a selective grazer, sequences of steps and bites performed by grazing waterbucks were measured and compared to existing datasets from wildebeest and Bohor reedbuck. This was based on the assumption that bouts of feeding (i.e. bites) and moving would differ in length and sequence according to whether a species was grazing a patch thoroughly (bulk) or picking out grass selectively.

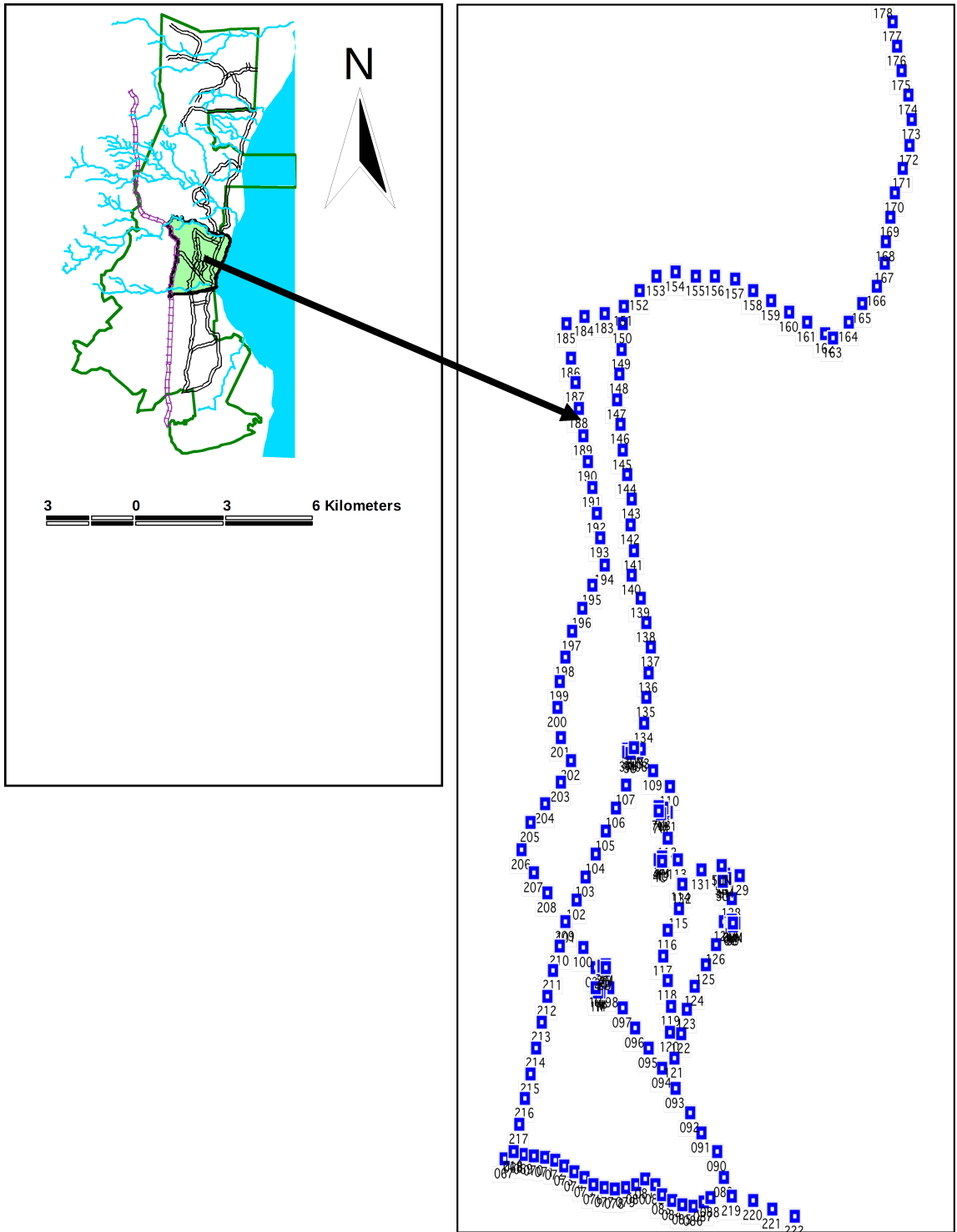


Figure 2: A map of Saadani North showing the standardized roads used for animal count

Source: Gutbrodt, (2006).

3.3 Data Collection

3.3.1 Use of burned versus non-burned patches

To measure the relative use of burned and non-burned areas by waterbuck compared to wildebeest and reedbuck, and possible shifts between the two over time, standardized road counts were used. A route covering most roads in the “Little Serengeti” area of SANAPA was selected, totalling a length of 20 km. Every 200 meters, on both sides of the route the following aspects were measured: sward height (3 categories; high, medium and low), woody vegetation cover (main species cover in 10% units) and the viewing distance (measured using a range finder) from road. That viewing distance was used for transect width which therefore changed every 200 m on both sides. The resulting rectangles of 200 m x visibility distance (m) were checked before the start of the counts whether they were burned. Any newly burnt rectangles on each count and the half burned rectangles were noted as well.

The route was driven 3 times a week (morning, afternoon, night with spotlights) and all grazers were counted on the rectangles. GPS location and behaviour (grazing, walking, standing, laying, running) of the animals were also recorded. If a newly burnt rectangle allowed for longer detection distances than before burning, the original width was retained and animals were only counted within that distance.

3.3.2 Pasture characteristics

(i) Grass species composition, height and cover

Non-burnt patches

Waterbuck, reedbuck and wildebeest actively grazing in non-burnt sites were sought randomly to assess characteristics of grazed sites. Upon sighting grazing individuals, the spot would be visited immediately for assessment. The assessment was based on 1m² plots

in which fresh biting marks were identified, and the following parameters were measured: total vegetation cover and height, total greenness (percentage of living vegetation), total grazing, grass-species composition, cover by species (live phytomass), grass species-specific height, grazing by grass species and distances to nearest tree and shrub. Greenness was recorded on a scale of 0-100% whereas height and grass cover were recorded following categories used by Western and Grimsdell (1979). The area grazed in a radius was also estimated in percent as it is expected that the wildebeest (relatively bulk grazers) will be feeding on a large area compared to the waterbuck and reedbuck. As the three species differ in their patch selection, wildebeest relying on predator detection in open areas with good sighting distance and the reedbuck relying on small bushes and tall grass to lie down and hide in case of danger, the distances to the nearby tree and bushes was also recorded. Nearby non-grazed control spots were identified randomly and assessed in the same way. A total of 20 replicates were assessed for each animal species.

Grazing within burnt patches

Grass species height and cover were also assessed in the burnt patches by seeking out animals grazing on burnt ground and immediately visiting the grazed spot for assessing a number of vegetation characteristics on a 1 m² plot. All parameters were measured and recorded as in part (i) above. However, grass species composition was difficult soon after burning as the sprouts were not easily identified. The same characteristics (except grazing) were assessed on a nearby non grazed 1 m² plot (as control) selected randomly on the burned patch. A total of 20 replicates were assessed for each animal species.

(ii) Nutritional quality of forage

Controlled burning was done at 7 open grassland sites in the area of Saadani North where most waterbuck occur. Each site contained 5 different plots (with a radius of 5 metres),

each with a different treatment (burned, cut, fertilized, cut and fertilized, control). Each treatment plot contained two randomly selected subplots of 50cm × 50cm where biomass was collected 2 times (once in the early and once in the late dry season), sorted into dead and live material and weighed (to assess the attractiveness of the area) (Hassan, 2007). The treatment plots were then assessed before and every 2 weeks after the burning on two 1m² plot (North and South) to assess effect of fire on grass species composition, grass structure and grazing. The live materials were dried in a solar oven for 2 days, weighed, pooled the 2 plots sample per treatment, grinded and analyzed for nutrient content. Grass samples were also harvested every 2 weeks in a period of 3 months after fire by clipping from randomly distributed 50cm x 50cm quadrants in each of the burned treatments to assess the effect of fire on grass nutritional quality. Similarly, grass samples were collected on the feeding and control plots of the three herbivores on the burnt areas and all together analysed to test whether these animals actively select the feeding sites based on nutrient quality. The samples were sorted by species, packed in paper bags and dried in the solar oven for 2 days before submission for laboratory chemical analysis in Switzerland.

3.2.3 Small-scale movement pattern of grazing waterbuck

It was assumed that bulk grazers and selective grazers would differ in their ways of alternating between bouts of feeding and walking. Because bulk grazers (in our case the wildebeest) need to graze patches more thoroughly than selective grazers, they should show longer bouts of grazing and thereby staying in one place while their heads lowered, or move over shorter distances with heads down during grazing. Selective grazers (reedbuck) should show shorter bouts of grazing alternating with short bouts of stepping forward, probably while holding their heads up. The waterbuck was expected to show an intermediate pattern of bout lengths between wildebeest and reedbuck.

To test for such differences, small-scale movements of wildebeest and reedbuck in SANAPA had already been studied in July-September, 2009 in relation to site and vegetation structure using the focal animal technique (Stähli, A. Unpublished data). In particular, grazing behaviour was compared by measuring bout sequences of bites and steps. A bout is defined as a short period of the same behaviour (Ruckstuhl *et al.*, 2003). These included bouts of biting off grass, but also bouts of stepping forward and bouts of standing still. Collecting the equivalent data on waterbuck was to test whether step-bite sequences in waterbuck are intermediate between reedbuck and wildebeest. Grazing waterbuck was observed from the car with binoculars. To avoid observer bias, observation distance did not exceed 150 m. Depending on the distance to the focal animal, the observer was waiting two to five minutes before starting data collection until the animal's grazing behaviour did not appear to be influenced by car presence.

Measurements were only taken from focal animals that were actively foraging, i.e. when searching for food or eating appeared to be a primary priority. As it is impossible to count all steps, the behaviour of the focal animal was recorded every four seconds for a maximum of 5 minutes according to one of four possibilities (head up/down; step/no step) and bout lengths calculated in units of 4 seconds. Depending on the visibility, movements of either front or hind legs were used for "stepping". If it was clearly noticeable that a feeding bout had ended or the animal was out of sight before the end of the 5min period, observation was stopped. As the nature of grazing movements depend on vegetation structure, the following data from the surrounding area of the focal animal (20 x 20 m) were also taken: a) vegetation type (classification from Tobler *et al.* (2003) was used), b) mean grass height in cm, and c) burning status (burnt/ non-burnt). Sample size reached was 40 bout series (5 min) equally distributed over the dry season 2010 (July to

September). As male and female may graze in different ways, the sex of the focal animal was also recorded.

3.4 Data Analyses

3.4.1 Use of burned versus non-burned patches by wildebeest, reedbuck and waterbuck

Chi square goodness of fit test was employed to test whether animals selected either patch type non-randomly. Trend analysis (regression) was also employed to test whether there was a shift in the relative abundance of animals from the non-burnt to the burnt areas (Field, 2009).

3.4.2 Pasture characteristics and nutritional quality of burnt and non-burnt patches in relation to grazing

The grass species occurred in very uneven frequencies on the plots. Therefore, those grasses that occurred infrequently (<20% of plots) and nowhere exceeded 5% cover were excluded from analysis. Moreover, t- test distribution was used to test whether the grass species clearly showed a difference in distribution between the feeding and control plots. To test for the difference of single parameters in the grazed plots between the three herbivores, one-way ANOVA was used for the variables that showed normal distribution pattern, and Kruskal-Wallis tests were used followed by a pair wise comparison by Mann Whitney U test for the variables that remained skewed even when transformations were employed.

A binary logistic regression was also performed to determine which variables best predicted the pasture characteristics as well as the distribution of the feeding and control plots (binomial dependent variable). Further, multicollinearity between variables was

checked by comparing variables using Spearman's correlation coefficients. Burned and non-burnt plots were treated separately, and 'Plot type' (feeding or control) was the dependent variable for each treatment. Covariate variables for the non-burnt plots were 'upper and lower height', 'cover of specific grass species', 'grass specific height', and '% greenness' whereas '% greenness', 'amount of green flush in %', 'height (upper and lower) and cover of the standing materials' were used for the burnt plots. Distances to the nearest bush, tree (acacia) and *Hyphaene* palm were used as covariates for both burnt and non-burnt plots. Nutrient concentration, digestibility and fibre concentration were expressed as percent dry weight of the grass sample material. SPSS version 12.0 was used in these analyses.

3.4.3 Foraging strategies of waterbuck in relation to wildebeest and reedbuck on non-burnt grassland

Comparison of bout length and steps per bout for three groups (3 animal species: reedbuck, Waterbuck, Wildebeest) was done using Kruskal Wallis test. In this case R program was used (R Core Team, 2004).

CHAPTER FOUR

4.0 RESULTS

4.1 Use of Burned Versus Non-Burned Patches by Wildebeest, Reedbuck and Waterbuck

At the beginning of the study, >50% of the study area was already burned and the burnt patch increased to 70% between first survey and the tenth survey (number of observations) (Fig. 3). The estimated average amount of green flush also slightly increased with an increase in number of surveys (observation time), however this increase was not significant.

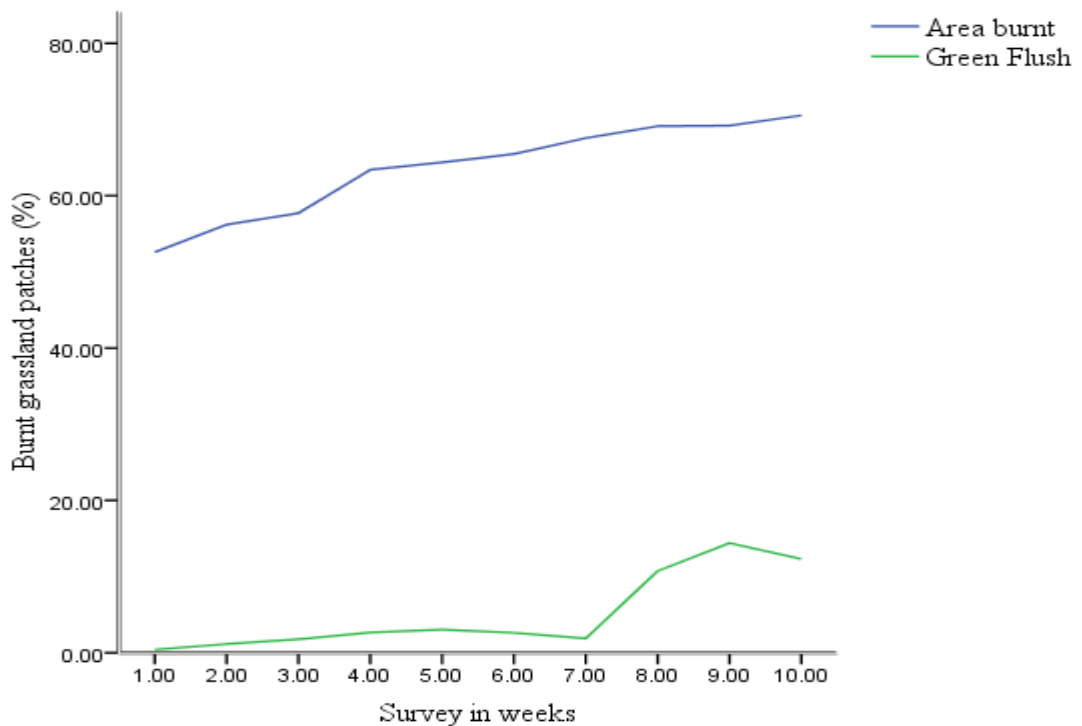


Figure 3: Percent increase in the burnt area and green flush with observation time

The number of reedbuck, waterbuck and wildebeest was not different between the two treatments (burnt and non-burnt). The difference between night and day time observations had no influence on distribution of waterbuck between burnt and non-burnt grassland patches as about 56.92% of the waterbuck seen during the day and 65.52% of those seen during the night were on the burnt areas whereas only 42.82% and 35.86% of the waterbuck seen during the day and night respectively were on the non burnt areas (Fig. 4). On the contrary, there was no increase in the density of reedbucks with increase in the size of burned areas (Appendix 1) though generally the density of reedbuck was higher in the burned areas compared to the non-burnt areas (Mann Whitney: $\chi^2 = 9.27$, $P = 0.002$). Similarly, the difference in time of the day had no effect on distribution of reedbuck (occurrence) between the treatments as about 73.8% of those seen during the day and 70.63% of those seen during the night were on the burnt areas, and only 25.7% and 29.37% of those seen during the day and night respectively were on the non burnt areas (Fig. 4). Wildebeest moved out of the study area soon after fire, resulting to very few sightings that were not worth statistical analysis and interpretation.

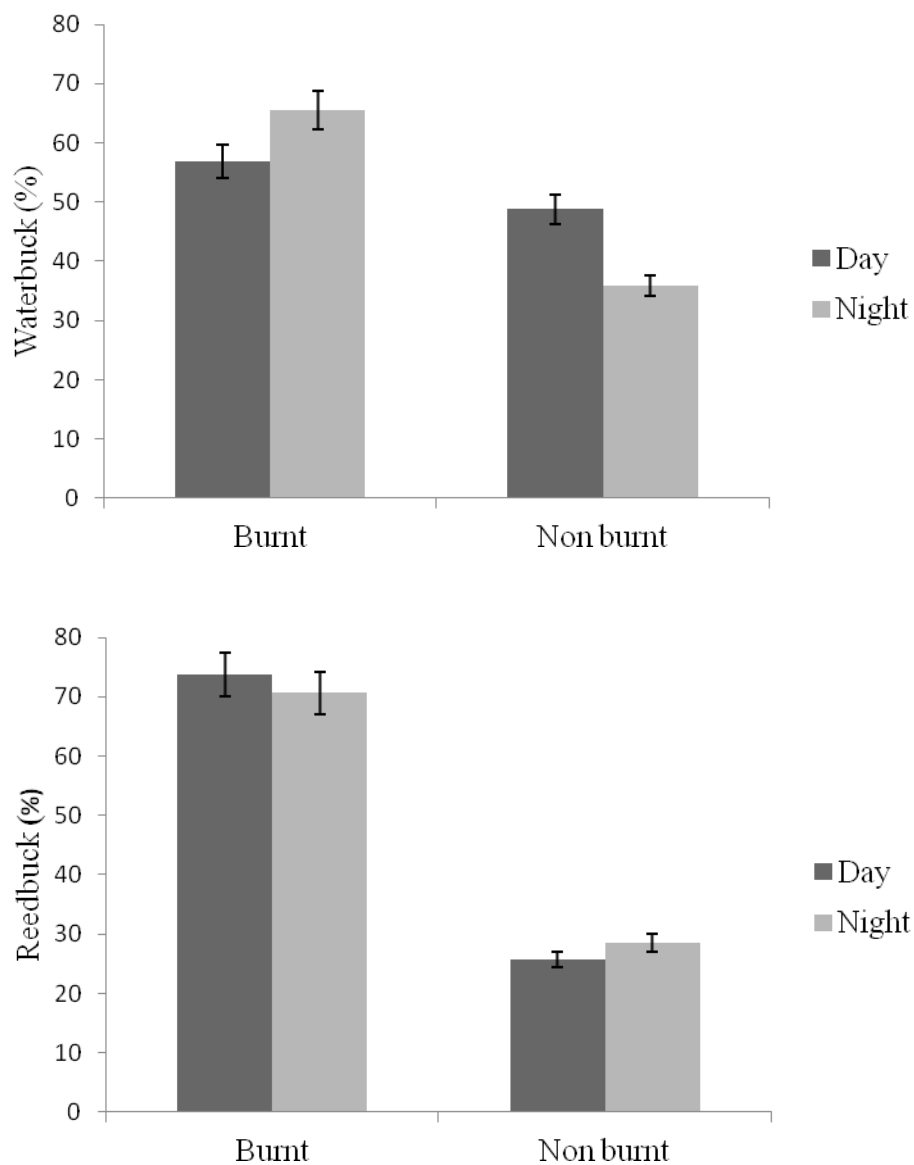


Figure 4: Number (in percentage) of waterbuck and reedbuck as observed in the burnt and non-burnt grassland patches during the day and night observations. Data represent means \pm SE.

4.2 Pasture Characteristics in Relation to Grazing

(i) Grass height and grass cover within non-burnt patches

The mean size of grazed patches (radius in meter) by the three herbivores differed significantly (Kruskal Wallis: $\chi^2 = 8.2$, $P = 0.016$). The wildebeest grazed relatively bigger patches than the other species, 3 times bigger than those of waterbuck and 4 times bigger than those of reedbuck (Appendix 2). Greenness and percent grazed (how much was grazed at the patches) of all grass species were not different except for *Panicum infestum* whose greenness and percent grazed significantly differed between the herbivores (Kruskal Wallis: $\chi^2 = 8.3$, $P = 0.015$ and $\chi^2 = 13.14$, $P = 0.001$) respectively. The wildebeest tended to graze more *Panicum infestum* as compared to waterbuck and reedbuck (Mann Whitney: $U = 21$, $r = -0.68$, $P = 0.001$ and $U = 26.5$, $r = -0.6$, $P = 0.001$), the waterbuck grazed the greener *Panicum infestum* as compare to wildebeest (Mann Whitney: $U = 50$, $r = -0.41$, $P = 0.03$) and the reedbuck grazed on greener *Panicum infestum* than that grazed by wildebeest (Mann Whitney: $U = 45$, $r = -0.5$, $P = 0.01$) but not significantly green than those grazed by waterbuck (Appendix, 2). The height of grazed tufts of *Panicum infestum* and *Echinochloa haploclada* also differed significantly between the three herbivores (Kruskal-Wallis: $\chi^2 = 20.18$, $P \leq 0.001$ and $\chi^2 = 5.82$, $P = 0.054$) respectively, being tallest in reedbuck and shortest in wildebeest (Appendix 2). However, there were no significant differences in other parameters such as ungrazed tuft height and the grazed tuft height of other grass species, the upper and lower grass height, distances to the nearest shrub and bush, total greenness and the cover by grass species of all the feeding plots of wildebeest, waterbuck and reedbuck.

Comparison between feeding and control sites

Appendix three presents the result of likelihood estimation of the binary logistic model indicating the important variables that differentiate the feeding and control (avoided) plots

of wildebeest. The overall model $\chi^2 = 68.50$ was significant at $P \leq 0.001$. This implies that the explanatory variables cover of *E. haploclada*, cover of *P. infestum*, height of the lower green grass sites, and the distance to the nearest small acacia are considered collectively influencing the selection of feeding sites. The pseudo R^2 of Cox and Snell R Square and Nagelkerke R Square were 0.40 and 0.534 respectively and about 76.9% of the sites were predicted correctly, the feeding and control plots were assigned 0 and 1 respectively. There were no significant models for the feeding and control plots of waterbuck and reedbuck, this implies the sites were not significant different.

(ii) Grass height and cover within burnt areas

A comparison between the feeding sites of the three herbivores in the burned area differed in the following parameters; Lower height of the dry grass (Kruskal Wallis: $\chi^2 = 7.33$, $P = 0.026$) and the percent cover of green flush (ANOVA: $F = 8.7$, $P \leq 0.001$), the latter being higher in the sites grazed by reedbuck than in those grazed by waterbuck and wildebeest (Bonferroni: $P \leq 0.001$ and $P = 0.05$) while the height of dry grass existed on the sites grazed by waterbuck only (Appendix, 2). Distance to the nearest small acacia (Kruskal Wallis: $\chi^2 = 7.68$, $P = 0.012$), the sites grazed by waterbuck had more trees than those grazed by wildebeest and reedbuck. Area grazed (Kruskal Wallis: $\chi^2 = 7.65$, $P = 0.022$), the wildebeest grazed 5 and 6 times big area as compare to the area grazed by reedbuck and waterbuck respectively. Cover of *P. infestum* (ANOVA: $F = 6.05$, $P = 0.004$), the reedbuck selected the sites highly covered with *P. infestum* as compare to those selected by waterbuck (Bonferroni: $P = 0.004$) but this selection did not differ to that of wildebeest and neither that of waterbuck and wildebeest differed. Percent tree cover (ANOVA: $F = 3.43$, $P = 0.039$), wildebeest were feeding on relatively open areas as compare to reedbuck and waterbuck. Percent greenness of *P. infestum* and other grass species (which were not easily identified at a young stage), we named them non *P. infestum*) also differed between

the herbivores (Kruskal Wallis: $\chi^2 = 22.15$, $P \leq 0.001$ and $\chi^2 = 10.25$, $P = 0.006$). The sites grazed by reedbuck had higher percent of *P. infestum* and non *P. infestum* greenness as compare to those grazed by waterbuck (Mann Whitney: $U = 57.5$, $r = -0.66$, $P \leq 0.001$ and $U = 71.5$, $r = -0.6$, $P \leq 0.001$) and those grazed by wildebeest (Mann Whitney: $U = 64$, $r = -0.54$, $P \leq 0.01$ and $U = 108$, $r = -0.48$, $P = 0.01$). Other parameters like the upper height of the dry materials, distance to the nearest bush and *hyphaene*, % cover of non *P. infestum* and % grazed of non *P. infestum* had no influence on the site selection. No models were generated for the difference between the burned feeding and control plots for both herbivores species, and no difference was observed between the two plots.

Nutritional quality of the grazed vs control sites in the burnt area

Feeding and control plots of the three herbivores showed no differences, neither in Neutral Detergent Fibre (NDF) content nor in the Acid Detergent Fibre (ADF) content of all grass samples. Only the nitrogen content differed between feeding and control plots of reedbuck (Fig. 3) (Paired t test: $t = 2.57$, $d = 13$, $P = 0.023$).

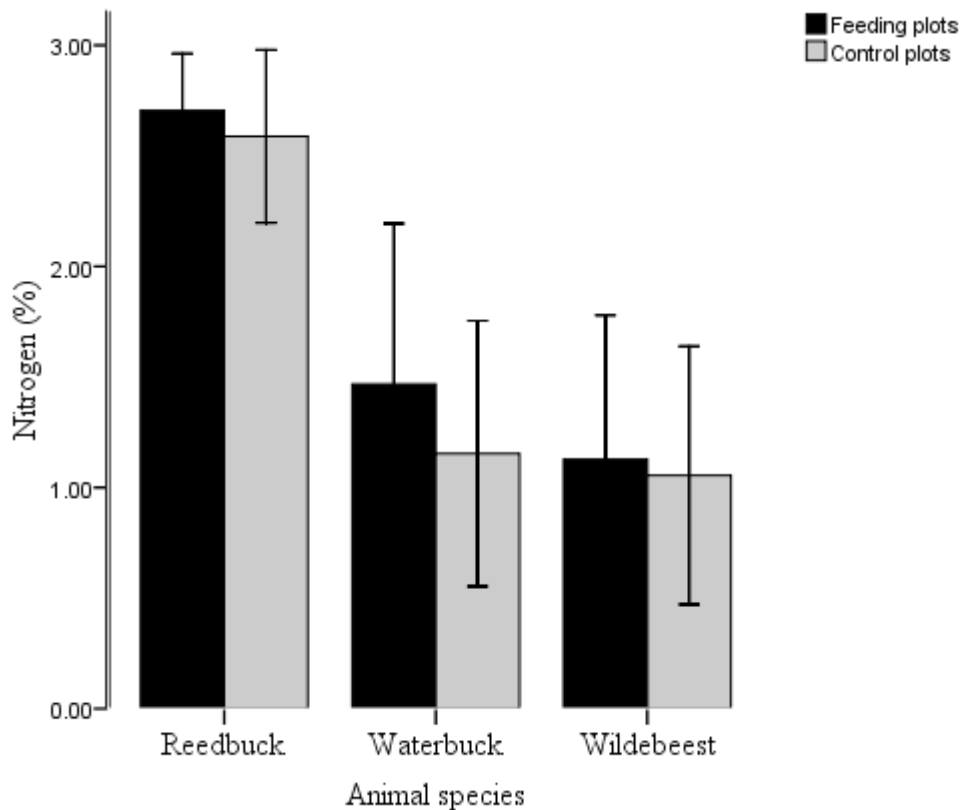


Figure 5: Mean percent of Nitrogen content (+ 1 SE) of the feeding and control plots as observed in the forage of the three herbivores Reedbuck, Waterbuck and Wildebeest feeding on the burnt grassland patches.

Moreover, nitrogen content of the grass samples collected in the feeding sites of reedbuck was higher than that found in the sites grazed by wildebeest and waterbuck (Mann Whitney: $U = 22$, $r = -0.61$, $P < 0.01$ and $U = 42$, $r = -0.46$, $P = 0.017$) respectively. The ADF also differed between sites grazed by the three herbivores (Table 1) with the reedbucks feeding on forage that had lower contents of indigestible parts of the forage, including lignin, cellulose, silica and insoluble forms of nitrogen (measured as Acid Detergent Fiber (ADF) as compare to waterbuck (Mann Whitney: $U = 32$, $r = -0.55$, $P = 0.004$) and wildebeest (Mann Whitney: $U = 17$, $r = -0.66$, $P = 0.001$) (Table 1). However, the structural components in plant cells (i.e. lignin, hemicelluloses and cellulose)

measured as Neutral Detergent Fiber (NDF) did not differ between the herbivores (Table 1).

Table 1: Nutrient content of the materials (\pm SE) collected from the burnt sites grazed by the Wildebeest, Waterbuck and Reedbuck as observed in Saadani north from July to September 2010, (χ^2 = Chi square,)

Nutrient content	Animal species			χ^2	P value
	Wildebeest	Reedbuck	Waterbuck		
Nitrogen % (N)	1.15 \pm 0.3	2.7 \pm 1.23	1.47 \pm 0.36	10.59	0.005
Neutral Detergent Fibre % (NDF)	71.31 \pm 2.19	64.89 \pm 0.49	71.65 \pm 2.01	5.44	0.06
Acid Detergent Fibre % (ADF)	53.8 \pm 1.11	47.41 \pm 0.63	52.98 \pm 1.23	12.89	0.002

(iii) Nutritional quality of the main forage grasses

Generally, grass samples collected 80 days after fire had higher N contents than samples collected before fire or after 180 days. Effect of fire had significant influence on the ADF. ADF concentration was higher in grass samples collected before fire and showed a minimum concentration in grass samples collected 80 days post fire (Table 2). ADF concentration was generally lower in *P. infestum* grass samples. NDF in the grass samples (biomass, *P. infestum* and *H. contortus*) differed significantly between sampling time but showed no difference within the same sampling time except for the samples collected 80 days after fire (Table 2).

Table 2: Concentration in percentage of N, NDF and ADF in percent dry weight \pm SE of biomass (gm) of all grass species and two preferred grass species collected before fire and at 80 and 180 days post fire in the burnt grassland patches

Sampling time	Element	Biomass	<i>P. infestum</i>	<i>H. contortus</i>	P value
Before fire	N	0.81 \pm 0.07	1.06 \pm 0.11	0.53 \pm 0.09	0.033*
	NDF	69.98 \pm 1.77	70.72 \pm 1.22	75.96 \pm 2.25	0.208
	ADF	56.3 \pm 0.65	56.14 \pm 0.75	59.28 \pm 0.89	0.107
80 days after fire	N	2.27 \pm 0.19	2.52 \pm 0.08	1.76 \pm 0.03	0.015*
	NDF	62.61 \pm 1.12	64.66 \pm 1.19	66.97 \pm 0.66	0.041*
	ADF	48.01 \pm 1.01	45.93 \pm 0.91	51.61 \pm 0.59	0.028*
180 days after fire	N	1.88 \pm 0.13	2.16 \pm 0.18	1.56 \pm 0.16	0.113
	NDF	66.02 \pm 1.37	64.09 \pm 1.64	67.76 \pm 0.53	0.341
	ADF	52.53 \pm 0.31	52.03 \pm 0.83	54.68 \pm 0.22	\leq 0.001**

* Significant at the 0.05 level; ** significant at $P \leq 0.001$ (Kruskal Wallis test)

4.3 Foraging strategies of waterbuck in comparison with wildebeest and reedbuck

There is a significant difference in foraging duration (steps with a head down) (Kruskal-Wallis, $H = 37.76$, $P < 0.001$) with reedbuck having significantly shorter foraging sessions (mean = 4.84 s \pm 0.14) than waterbuck (mean = 7.19 \pm 0.29) or wildebeest (mean = 6.42 \pm 0.28) (PostHoc: $P < 0.05$). Similarly, the duration in grazing (head down without a step) differed between species (Kruskal-Wallis, $H = 14.05$, $P = 0.001$) with reedbuck having significantly shorter grazing sessions (mean=11.97 \pm 0.6) than waterbuck (mean=16.83 \pm 0.85) or wildebeest (12.12 \pm 0.64) (PostHoc: $P < 0.05$), and the duration in moving (step with the head up) (Kruskal-Wallis, $H = 11.32$, $P = 0.003$) with reedbuck having significantly shorter moving sessions (mean = 5.71 \pm 0.64) than waterbuck (mean=9.63 \pm 0.85) or wildebeest (5.9 \pm 0.65) (PostHoc: $P < 0.05$), where as there was no significant difference in the duration of standing (head up without a step) (Kruskal-Wallis, $H = 0.35$, $df = 2$, $P = 0.8405$) and the variation in standing sessions for each individual were as follows; reedbuck (mean= 9.81 \pm 0.67), waterbuck (mean= 10.72 \pm 0.75) and wildebeest (10.33 \pm 1.14) (Fig. 6).

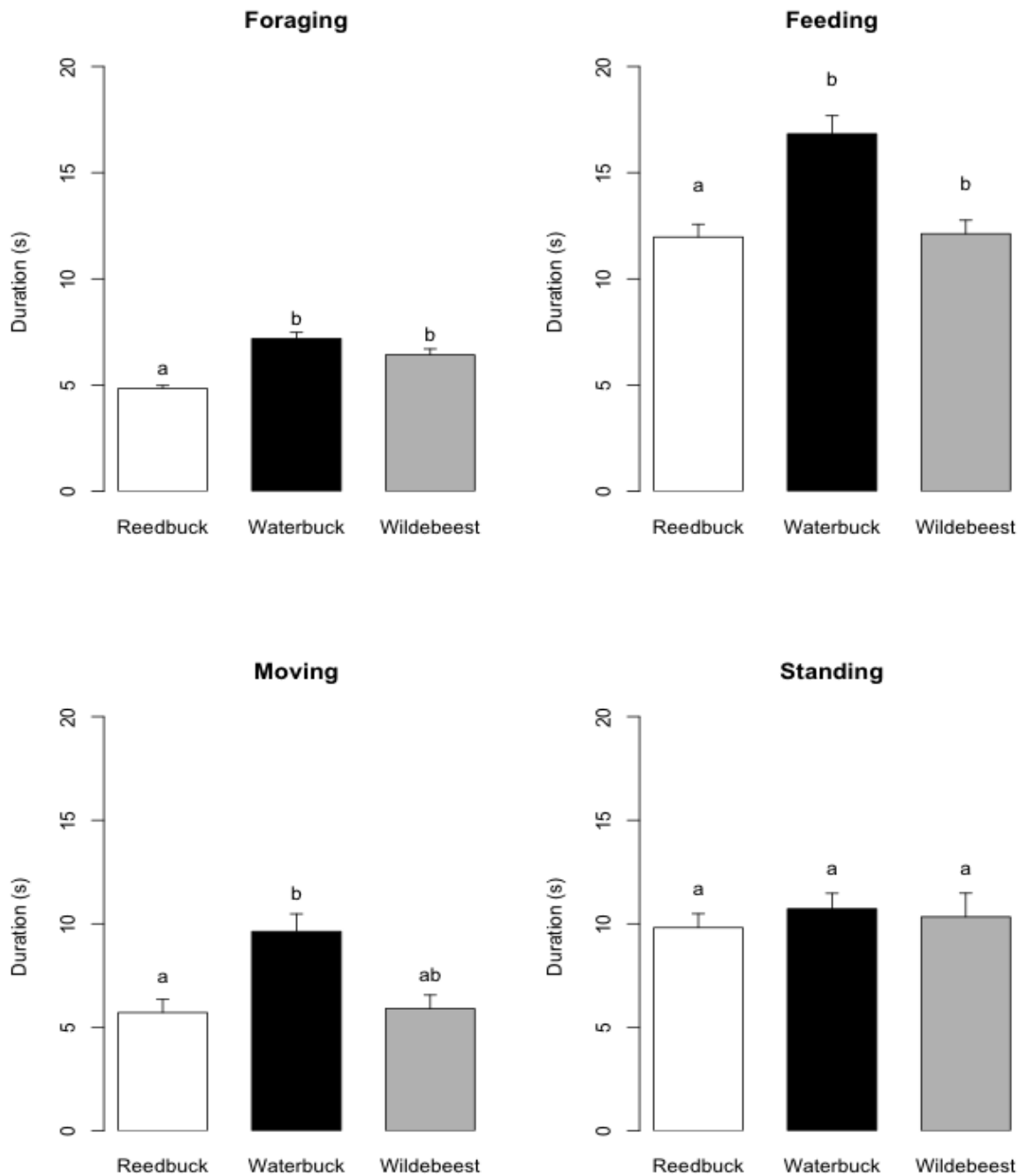


Figure 6: Bout length of different behaviours (Foraging, Feeding, Moving and Standing) of Reedbuck, Waterbuck and Wildebeest as observed in Saadani north during the dry season. Arrow bars indicate standard error. Letters indicate significant differences among species.

Feeding environment

The estimated grass heights of the feeding sites used by wildebeest, waterbuck and reedbuck differ from each other considerably (ANOVA: $F = 4.06$, $P = 0.02$). As assumed, the wildebeest preferred to feed in short-grass ($44.8\text{cm} \pm 3.52$) while the reedbuck and waterbuck preferred relatively tall-grass areas of ($53.33\text{cm} \pm 2.9$) and ($57.00\text{cm} \pm 2.86$) means respectively. However, this difference was only significant between waterbuck and wildebeest (Tukey HSD: $P = 0.019$). Bush cover of the sites used by the three herbivores differed significantly (ANOVA: $P \leq 0.001$), the waterbuck in this case were seen on the bushy areas as compare to wildebeest (Tukey HSD: $P = 0.003$) as well as reedbuck (Tukey HSD: $P \leq 0.001$).

CHAPTER FIVE

5.0 DISCUSSION

5.1 Use of burned versus non-burned patches by wildebeest, reedbuck and waterbuck

The distribution of herbivores species between the two grassland patches did not show a biased distribution to the burned patches. Hobbs (1991) and Archibald *et al.* (2005) also suggested that, when the area is burned it is not necessarily that grazers would only spread more widely within the burned area but may also be "vacuumed" off unburned grazed patches unless fires were frequent and large enough to cover even the grazing lawn created by these grazers.

A time wise (day and night) analysis taking the individual species distribution pattern with respect to time of the day also did not show any difference. We expected that, since the reedbuck is hiding species they will not be easily seen in the non burnt areas as plant cover will offers concealment during the day time and expected to see them easily by spotting them during night. However the results could not explain this. The number of reedbuck and waterbuck was higher in the burnt areas despite of the observation time. This suggests that, their higher number in the burned areas contrary to non-burnt could be due to the higher visibility of these areas. On the other hand, wildebeests moved away from burnt patches as the area got progressively burned (Appendix 1). This may be associated with the fact that wildebeest feed selectively at a landscape scale, visiting the same preferred patches every season (Melton, 1987; Wilmshurt *et al.*, 1999; Fryxell *et al.*, 2005). By doing this they create the so called "grazing lawns" so as to maintain and secure their food resources. Therefore, their absence in the study area would be interpreted that they moved to other places where they have these grassland patches of secure food during that season,

also it could be referred as a seasonal migration pattern as it is for Serengeti National Park. This fact limits this study from making reasonable account on the distribution of this species. Moreover, when it was assessed whether there was a trend in increase in the number of waterbuck, wildebeest and reedbuck in the burned areas, a trend was seen in waterbuck only whereas reedbuck and wildebeest did not show any. These results are associated with a number of reasons: first, animals like reedbuck are territorial animals where as the territories of waterbuck and wildebeest are larger and tolerate other individuals to some degree (Estes, 1991). Therefore, having seen reedbucks in the burned areas mostly does not imply that they preferred these places to the non-burnt areas, rather they are maintaining their territories, thus their mobility has been limited by this behaviour. However, these findings also contradicts the idea that reedbuck would shun burnt areas to limit predation risk as they require a certain amount of cover (Estes, 1991).

5.2 Pasture characteristics and nutritional quality

(i) Pasture characteristics of burnt and non-burnt patches in relation to grazing

Results presented in this study indicate that the wildebeest (bulk grazer) has a wider grazing circle in both grassland patches (burnt and non-burnt), followed by the waterbuck and the reedbuck having grazed on the smallest area per observation (Appendix 2). Similarly, as expected, the grazing height of the reedbuck was higher compared to that grazed by waterbuck, and was shorter than that grazed by wildebeest (Appendix 2). This is because, as the bulk grazers wildebeest tend to feed in one place over a long time and move seasonally between areas having high nutritious grasses at that time instead of switching between particularly nutritious species within a community in the same area (Benshahar and Coe, 1992). With this behaviour they create large grazing circles and with repeated grazing they create the short grassland patches of high digestive quality which are known as grazing lawns (McNaughton, 1976)

Greenness of grass in the burnt and non-burnt grassland patches was also another key determinant of feeding site selection by the three grazers with all species associating with a relatively greener grass sward while avoiding senescent and lignified sward which is also regarded as less nutritious to ungulates (Sinclair, 1975). However, reedbuck tends to select sites that had higher nutritious forage (in terms of greenness) as compare to the other species (Appendix 2). The findings therefore are in line with other findings elsewhere that many ungulate species prefer green vegetation during the dry season (Bell, 1971, Sinclair and Norton-Griffiths 1979), and also with the fact that migratory wildebeest (*Connochaetes sp.*) in the Serengeti region are regulated by the amount of green grass available during the dry season (Bell, 1971; Sinclair, 1985).

In Uganda, the kob (*Kobus kob*) distribution has been associated with green grass abundance, and it has been revealed to be particularly important in the dry season (Deutsch, 1994). Green vegetation contains more water than withered grass (Georgiadis and McNaughton, 1990). The high preference for sites with green sward may therefore be a behavioural adaptation to meet both water and energy requirements during dry seasons. On the other hand, observations made on the burnt patches show that the waterbuck were mainly feeding on the dead standing materials left after fire (personal observation). However, the nutrient analysis carried out could not explain much about this preference but, Hassan (2007) found increased nutrient concentrations, low ADF and high *in vitro* organic matter digestibility in post-burn standing dead material. The higher nutrient availability in the standing dead materials could be because of weak translocation of nutrients to storage due to wilting of the plant (Millard and Proe, 1991). This could in one way tell why these herbivores preferred these standing materials to the non-burnt patches. Forage quality was equally important for selection of feeding sites by reedbuck. Together with the selection of sites with green phytomass in the non-burnt patches, they tend to

select areas of higher green flush (regrowth) in the burnt areas as compare to wildebeest and waterbuck.

The finding in this study corresponds to the fact that the selection of post-fire regrowth by herbivores may be governed by body weight (Wilsey, 1996). Since the small herbivore species need higher quality food than large herbivores, it would be expected to find small species to be restricted to recently burned sites or areas with low amounts of dead stem material compared to those used by the larger animals (Traill and Bigalke, 2006). This is because the larger species have longer gut retention times than smaller species, allowing better digestion and extraction of nutrient from low quality food (Prins and Olf, 1998; Gordon and Illius, 1996).

Biomass of a particular forage resource could be another important factor in explaining the preference (in terms of site coverage and grazing) for *Panicum infestum* observed in the feeding sites of wildebeest and also of the other animal species in the dry season. *Panicum infestum* constitutes a large proportion of the vegetation during this period. Rohrer (2007) also found preference to the same grass species in waterbuck, wildebeest and reedbuck in the early dry season but this preference switched to *Heteropogon contortus* and *Waltheria indica* in late dry season despite its low proportion in all vegetation types.

However, the higher selection of *Panicum infestum* shown by wildebeests compare to other species does not necessarily imply that they prefer this grass species more than the other herbivores, rather it can be explained by the unselective nature of wildebeest and that they were mainly feeding proportionally on what is available. Besides selection for high quality forage, ungulates may also select burned areas because of improved visibility and hence, reduced risk of predation (Moe and Wegge, 1997). The data show avoidance of

high tree cover by reedbuck and wildebeest but preference by waterbuck. This may be an anti-predatory behaviour for wildebeest (Lamprey, 1963; Estes, 1991) where as for the waterbuck it comply with other findings that in the dry season they prefer medium density wooded areas which would offer a scanty shade during the day (Spinage, 1982).

A binary logistic regression output shows that the lower the grass height, increased distance to small bushes, decrease in the cover of *E. haploclada* and *P. infestum* and the increase in the cover of *S. pyramidalis* would determine the feeding and the avoided plots (control plots) of wildebeest (Appendix, 3). The cover of *E. haploclada* and *P. infestum* would determine the feeding plots whereas the control plots would be determined by lower grass height, distance to small bushes and cover of *S. pyramidalis*.

(ii) Nutritional quality of the main forage species

The study demonstrates that post fire above ground regrowth had higher Nitrogen concentrations than unburned vegetation. Eighty days (two months and two weeks) after burning, post fire regrowth had higher mean Nitrogen as compare to the samples collected before fire (mean difference: 1.46 Nitrogen in *P. infestum*, 1.23 Nitrogen in *H. contortus* and 1.46 Nitrogen in the biomass), but after six months, concentrations had declined. These results concur with previous research reported from elsewhere, e.g. the Maasai steppe, an ecosystem adjacent to Serengeti, where enhanced concentrations of N occurred one month after fire and the enhancement was short lived, decreasing to the same level as the control by the end of three months after fire (Van de Vijver *et al.*, 1999). Thus the time of commencement of the enhancement effect on N reported in this study is comparable to that found by Van de Vijver *et al.* (1999).

However, this increase in N concentration may also be associated with other processes related to the plant-soil N circulation such as the presence of acacias which live in

symbiosis with nitrogen fixing bacteria, which could enhance availability of nitrogen in the soil for themselves and neighbouring plants (Cochard, 2004). Similarly, the observed effect might also be related to the interactive effect of fire and herbivory causing continued rejuvenation from grazing and/or deposition of N in herbivore urine which can be larger in burnt than in non-burnt areas if herbivores are more attracted to burnt patches (Tomor and Owen-Smith, 2002). In addition, Fisher and Binkley (2000) have shown that the addition of ash to soil and increased microbial mineralization rate after fire can cause the build up of ammonium. Thus this higher N concentration could be due to fire enhanced organic matter mineralization.

The significantly higher ADF in samples collected before fire than those collected after fire suggests that regrowth after fire contains fewer amounts of structural carbohydrates thus would be good animals' feed. Low concentration of ADF for all grass samples collected in 80 days after fire may be caused by fresh growth in burnt areas and low ADF concentration in the young biomass (Norton-Griffiths *et al.*, 1975). Nutritional value of the samples was expected to decline with time after fire because more fibrous material would normally build up with maturation stage (Milford and Minson, 1966; Pratt and Gwynne, 1997) and that is what has been observed in the samples collected in 180 days after fire (Table 2).

It is well known that high quality in forage refers to high N concentration, high digestibility, high mineral level and low ADF concentration (Hanley *et al.*, 1992; Hassan *et al.*, 2007). Reduced ADF and enhanced digestibility enable herbivores grazing in burnt areas to maximize both daily energy and nutrient intake (Fryxell, 1991) because a high overall intake of fibres reduces the extent of digestibility of each food particle (Smith, 1995).

5.3 Foraging strategies of waterbuck on non-burnt patches in comparison with wildebeest and reedbuck

The mean bout lengths (sessions of each behaviour) of waterbuck was not intermediate between the reedbuck and wildebeest as expected rather was longer than all. They spend more time with their head down searching for food and eating than the reedbuck as well as the wildebeest thus taking longer time until they move from their feeding spot with their head up. This would mean that their feeding bouts (behaviours) does not differ much from that of bulk grazers (wildebeest, where they would make relatively higher number of steps with its head down as compare to the selective grazers) and that once they have found a suitable feeding patch, they eat the grass more thoroughly from the spot. In his study Rohrer (2007) also found that reedbuck was the most selective of these three ruminants, and that waterbuck feeds on the same plant species like wildebeest, but more selective on nutrient-rich individuals or plant parts. This would support our belief that most of the grazing lawns in Saadani are not due to wildebeest but to waterbuck.

The reedbuck having shown the shortest bout sessions could be explained by the fact that reedbuck when feeding select only single plants, and then they would try to find the nearest suitable plants while lifting the head up, still eating the current one. In contrast, the bulk grazers would finish the whole patch before moving to the next one. Moreover, the environment of feeding differed between the herbivores. The bulk grazer, wildebeest was usually found in short grass areas whereas the waterbuck and reedbuck were found on relatively tall grass areas.

CHAPTER SIX

6.0 CONCLUSIONS AND RECOMMENDATION

6.1 Conclusions

This study reaches four key conclusions

- (i) Fire leads to unequal distribution of large herbivores between burnt and non-burnt grassland patches.
- (ii) Grazed patches are actively selected for feeding.
- (iii) Fire increases quality of forage through increased Nitrogen and decreased NDF and ADF.
- (iv) Waterbuck was found not to be an intermediate grazer between wildebeest, a bulk grazer and Bohor reedbuck, a selective grazer.

6.2 Recommendation

Fire is an important adaptive management strategy for savannah grassland like Saadani National Park but its use should follow a given Fire Management Plan. The plan should synchronise the extent of burning and the time of burning in the season to cater for availability of other high-quality grass swards such as grazing lawns.

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APPENDICES

Appendix 1: Density of waterbuck, reedbucks and wildebeest as observed in the burnt and non burnt grassland patches in Saadani National Park from July to September 2010

Survey in weeks	Treatment	Area observed (ha)	Waterbuck density	Reedbuck density	Wildebeest density
1	Burnt	314	21.67	20.00	19.08
	Non burnt	283.2	35.08	6.92	8.50
2	Burnt	335.6	13.79	18.71	19.33
	Non burnt	261.6	24.25	16.25	0.00
3	Burnt	344.6	48.13	22.83	29.67
	Non burnt	252.6	26.67	26.75	0.00
4	Burnt	378.6	30.92	34.00	0.00
	Non burnt	218.6	27.50	15.33	0.00
5	Burnt	384.4	25.21	28.83	0.00
	Non burnt	212.8	42.42	32.58	2.50
6	Burnt	391	34.21	17.83	0.00
	Non burnt	206.2	3.38	28.25	0.00
7	Burnt	403.4	14.46	14.83	3.50
	Non burnt	193.8	18.58	1.96	0.00
8	Burnt	412.8	79.58	79.25	8.00
	Non burnt	184.4	11.88	11.25	0.00
9	Burnt	413.2	21.58	26.71	0.00
	Non burnt	184	23.00	20.17	0.00
10	Burnt	421.2	77.38	88.21	0.00
	Non burnt	176	26.50	35.96	0.00
Mean	Burnt	22898.1	0.2129	0.2224	0.0081
	Non burnt	15736.4	0.1772	0.1448	0.0482

Appendix 2: Mean \pm Standard Error of grazed area (square metres) and grazed and ungrazed tuft height (centimetres) of different grass species of the feeding plots of wildebeest, waterbuck and reedbuck as observed in the Saadani North area from July to September 2010.

Treatment	Variable	Animal species			P value	
		Wildebeest	Waterbuck	Reedbuck		
Unburnt	Grazed area radius	9.6 \pm 3.28	3.15 \pm 0.93	2.22 \pm 0.47	0.016	
	<i>Panicum infestum</i> , grazed height	4.91 \pm 0.53	14.33 \pm 2.55	17.06 \pm 2.2	\leq 0.001	
	<i>Echinochloa</i> <i>haploclada</i> , grazed height	10.33 \pm 4.84	21 \pm 3.81	39.8 \pm 7.42	0.054	
	<i>Panicum infestum</i> , % grazed	89.55 \pm 4.23	68 \pm 5.36	65.59 \pm 5.52	0.001	
	<i>Panicum infestum</i> , % greenness	24.58 \pm 6.12	44.06 \pm 5.63	50 \pm 5.58	0.015	
	Burnt	Dry grass, height	0	1.91 \pm 2.92	0	0.026
		Green flush, %	4.11 \pm 0.98	2.21 \pm 0.68	7.22 \pm 0.99	\leq 0.001
		Distance to a small acacia	17.4 \pm 4.1	29.66 \pm 7.3	8.74 \pm 2.9	0.021
		Tree cover %	12.11 \pm 2.30	18.96 \pm 2.45	11.73 \pm 1.88	0.039
		Area grazed radius	17.47 \pm 4.56	2.92 \pm 0.73	3.65 \pm 1.15	0.022
<i>Panicum infestum</i> , cover %		13.83 \pm 2.1	7.22 \pm 3.28	16.24 \pm 1.18	0.004	
Non <i>Panicum infestum</i> , % greenness		21.47 \pm 6.18	18.93 \pm 7.04	43.18 \pm 5.55	0.006	
<i>Panicum infestum</i> , % greenness	16.56 \pm 4.51	11.9 \pm 4.7	43.41 \pm 4.94	\leq 0.001		

Appendix 3: Effect of explanatory variables of wildebeest's feeding and control plots.

The model was ranked best based on its ability to predict the difference between the two plots

Variables	B	S.E.	Wald	Sig.	Exp(B)	95.0% C.I.for
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						exp (B)	
						Lower	Upper
Lower green height	.059	.014	18.876	.000	1.061	1.033	1.089
Distance to a small bush	.020	.010	3.835	.050	1.020	1.000	1.040
<i>Echinochloa</i> <i>haploclada</i> , cover %	-.178	.081	4.790	.029	.837	.714	.982
<i>Panicum infestum</i> , cover %	-.088	.023	14.263	.000	.916	.875	.959
<i>Sporobulus</i> <i>pyramidalis</i> , cover %	.298	.170	3.078	.079	1.348	.966	1.881
Constant	-1.253	.473	7.016	.008	.286		

Where B=Estimated regression coefficient, S.E= Standard Error, Wald = Wald statistic, Exp (B) = Odd ratio, and C.I = Confidence Interval at 5% level of significance