DETERMINING THE ROLE AND RELATIVE IMPORTANCE OF PREDATOR AVOIDANCE AND NUTRITION AS PROCESSES INFLUENCING HERBIVORE UTILISATION OF BURNT AREAS IN SATARA, KRUGER NATIONAL PARK, SOUTH AFRICA

By Zoë Luhdo

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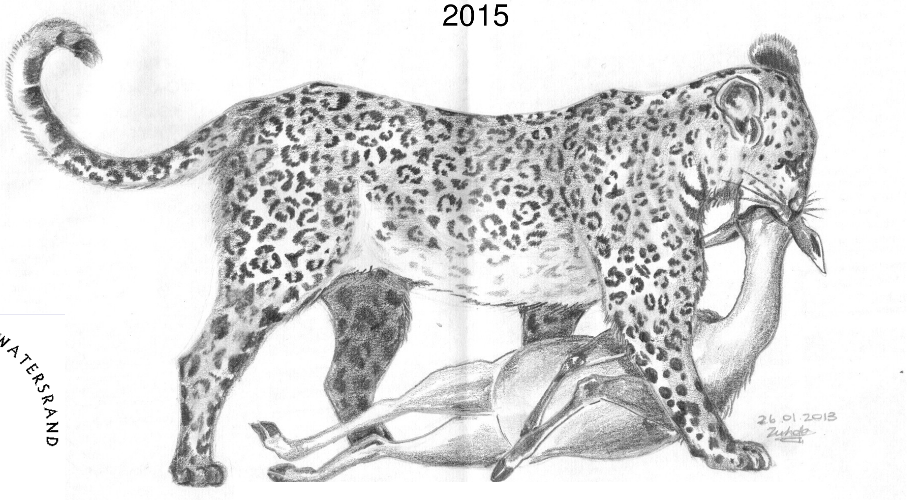

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PREFACE

The experimental work described in this dissertation was carried out in the School of Animal, Plants and Environmental Sciences, University of Witwatersrand, Johannesburg, from January 2013 to February 2014, under the supervision of Dr Sally Archibald (School of Animal Plants and Environmental Science, University of Witwatersrand, Johannesburg) and co-supervised by Dr Kate Parr (Lecturer in ecology, School of Environmental Sciences, University of Liverpool, Liverpool) and Mrs Navashni Govender (Programme manager: Fire ecology & Biogeochemistry, SANParks, Scientific Services, Kruger National Parks, South Africa). These studies represent the original work of the author and have not been submitted in any form for any degree or diploma at any University.

Signed:

Luhdo

Z. Luhdo (Candidate)

Signed:

Dr Sally Archibald (Supervisor)

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PLAGIARISM DECLARATION

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1. **I am aware that plagiarism (the use of someone else's work without their permission and/or without acknowledging the original source) is wrong.**
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ABSTRACT

This study aimed to determine the role and relative importance of predator avoidance and nutrition as processes influencing herbivore utilisation of burnt areas, at Satara, Kruger National Park by using variation in fire size and fire season. The driving factors investigated included forage quality, forage quantity, vegetation structure and predation risk.

The effect of fire size and season on the landscape was tested by recording grass height, greenness, grass nutrient sampling and visibility. Results showed that fire size and season had a significant impact on the physical environment by decreasing grass/forage quantity post-fire but increasing grass/forage quality. Over time the plots returned to near pre-fire conditions, with forage quantity increasing (grass height and biomass) and forage quality decreasing (nitrogen availability). Visibility increased immediately post-fire, more significantly in regards to herbivores with their heads in a "head-down/grazing" position than in a "head raised/vigilant" position. As with forage quantity and quality, visibility returned to near pre-fire conditions at the end of the study sampling period. The response of animals to these changes in the environment was recorded through dung counts, camera traps and behavioural observations. I found that there was increased use of burnt plots post-fire through comparing herbivore presence on plots burned in different sizes and seasons, day/night utilisation of plots, and using behaviour data I could determine to what extent forage and predation risk were driving the use of burnt areas. I focused on three herbivore species (*Aepyceros melampus, Connochaetes taurinus* and *Equus quagga)* which varied in terms of body size digestive systems, forage type, and social behaviour. As expected, I found that predation risk did appear to be more important in driving the behaviour of the smaller-bodied herbivores but both nutrient requirements and susceptibility to predation were shown to play a role in explaining the use of burnt areas for all three herbivore species. Variation between plots in environmental factors such as tree density, forb percentage and distance to water, were found to be not significant and thus did not confound our results.

Key words: Forage quality, forage quantity, predation risk, pyric-herbivory, fire size, fire season, vigilance.

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1 CHAPTER 1: GENERAL INTRODUCTION

1.1 Literature review

The properties of ecosystems are determined by a variety of factors including climate, soil and disturbances (Bond & Keeley, 2005). Variation in the duration, intensity and recurrence of disturbances are important in determining levels of diversity (McNaughton, 1992) and influencing vegetation structure (Archibald et al., 2005; Thonicke et al., 2001).

Savanna ecosystems are characterised by a discontinuous layer of trees and shrubs and a continuous layer of grasses (Scholes & Walker, 1993; Van Langevelde et al., 2003). Two of the most important disturbances influencing the structure of savannas are fire and herbivory (Alder, Raff & Lauenroth, 2001; Anderson et al., 2007; Collins & Smith, 2006; Yarnell et al., 2007). Fire and herbivory both consume above-ground biomass and each have been studied extensively as separate disturbances (Bond & Keeley, 2005; Alder & Lauenroth, 2001, McNaughton, 1992). However minimal research has been done regarding the synergies between them (Archibald et al., 2005; Fuhlendorf et al., 2008). The feedbacks between fire and herbivory are important in maintaining heterogeneity within savanna ecosystems (Allred et al., 2011; Kerby et al., 2007) as well as influencing landscape structure on both a coarse and fine scale (Eby et al., 2014; Shackleton & Scholes, 2000).

Fire is a non-selective consumer, removing most moribund material. This decreases grass height and stimulates grass re-growth, also referred to as a green-flush (Allred et al., 2011; McNaughton, 1983). Fire behaviour is influenced by weather conditions, as well as vegetation and fuel properties (Klop et al., 2007; Rutherford et al., 2006; Tainton & Hardy, 1999; Huntley et al., 1984). This variation in fire characteristics and its impact on the surrounding landscape will be further discussed in Chapter 3. Fire is known to influence forage quantity (how much forage is available post-fire, how much re-growth is stimulated) (Bond & Keeley, 2005), forage quality (Eby et al., 2014; Van de Vijver et al., 1999) and vegetation structure (grass height and tree density) (Eby et al; 2014).

Grazing influences the spatial heterogeneity of vegetation; however this impact depends on the interaction between the spatial patterns of grazing and the spatial patterns of vegetation (Adler et al., 2001; Milchunas & Lauenroth, 1993; Yarnell et al., 2007). Grazing stimulates above ground production of grass (McNaughton, 1983; Milchunas & Lauenroth, 1993) and can increase grass quality (stimulating grass re-growth which has a higher nutrient content) (Alder & Lauenroth, 2001; Fuhlendorf & Engle, 2004; Moe & Wegge, 1997; Mutanga et al., 2004; Verweij et al., 2006) and grass quantity (recycling of plant nutrients promotes plant growth) (De Mazancourt et al., 1991; Verweij et al., 2006). Continuous heavy grazing can sometimes result in a community switch to "lawn grasses" that are grazing tolerant and highly productive (Hempson et al., 2014). In other circumstances degradation (loss of grass cover and a switch to less palatable species) can occur (Tainton, 1972).

The interaction between fire and herbivory is known as pyric-herbivory (Fuhlendorf et al., 2008). There are various positive and negative feedbacks between fire and herbivory, each of which is scale dependant and can increase or decrease spatial or temporal heterogeneity in the landscape (Collins & Smith, 2006). Herbivores have been found to adjust their foraging strategies as a response to fire (Kerby et al., 2007). Because animals are attracted to the post-fire landscape, fires should either concentrate or disperse grazers depending on the size of the fire (Archibald et al., 2005). How long this lasts depends on whether grazers continue to keep the grass short. In turn grazers can influence fire by consuming fuel and reducing fuel loads and continuity (Allred et al., 2011; Archibald et al., 2005). Grazing pressure on burnt areas is determined by the size and number of fires and grazers, as well as the herbivores' need for resources (Fuhlendorf et al., 2008). Time since burn affects grazer attraction as vegetation changes occur (Figure 1.1).

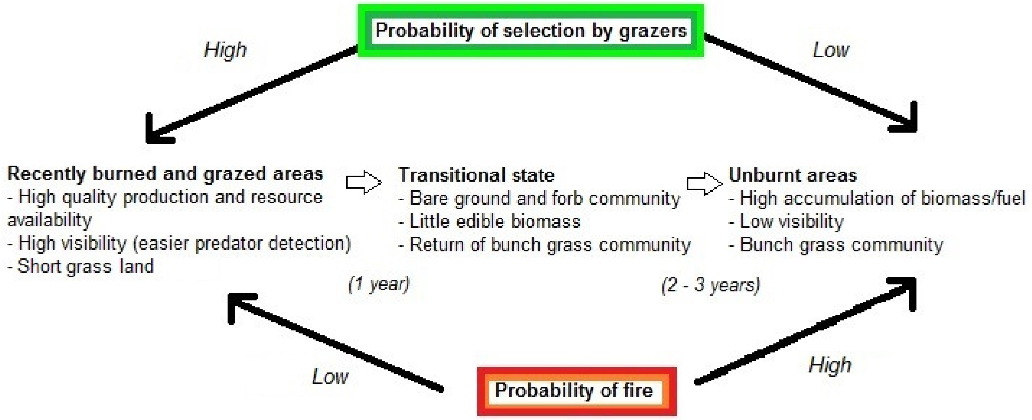


Figure 1.1 Diagram indicating short-term interactions between fire and grazing: the probability of an area being selected by grazers verses the probability of fire based on time-since-fire (adapted from Fuhlendorf et al., 2008).

On a short-timescale, fire initially decreases grass height and stimulates re-growth. How long the grass remains short depends on grazing intensity, rate of re-growth (constant cropping stimulates re-growth) (McNaughton, 1992) and grass quality (Anderson et al., 2010; Van der Waal et al., 2011). Areas where grazing pressure has been maintained and short, grazing tolerant lawn grass community persists, are known as a grazing lawn (Cromsigt & Kuijer, 2011; Cromsigt & Olff, 2008; Hempson et al., 2014). Ultimately the length of time grass is kept short will determine which grass community (tall, grazing intolerant bunch grass or short, grazing tolerant lawn grass) will dominate (Anderson et al., 2010; Archibald et al., 2008; Cromsigt and Olff, 2008;Swain et al., 2007) (Figure 1.2). Spatial variability in grazing pressure determines the balance between the utilisation of burnt areas and the maintenance of burnt areas (Fuhlendorf & Engle, 2004).

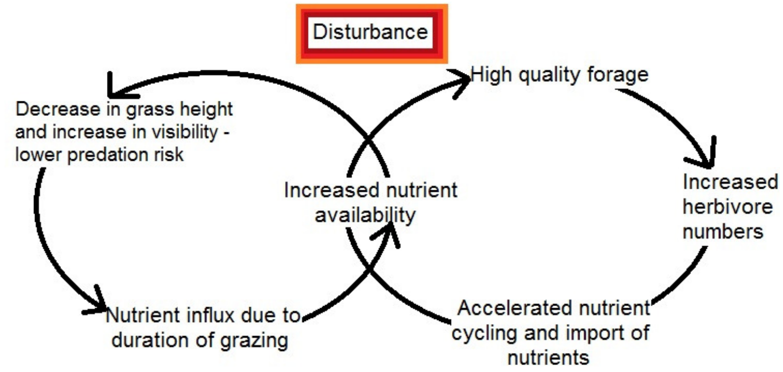


Figure 1.2 Influence of fire in the short term and herbivory in the long term on forage quality and quantity and visibility/predation risk (adapted from Anderson et al., 2010 and Fuhlendorf et al., 2008).

A major research question is what stimulates the formation of grazing lawns. Some argue that grazing lawns only occur in sites that have particular soil characteristics (based either on their landscape/geology e.g. sodic sites (Grant & Scholes, 2006), or due to past human influence e.g. old cattle kraals (Young et al., 1995)). It has also been suggested that short grass alone can initiate a positive feedback with grazing and nutrient cycling to produce grazing lawns. This is because short grass areas offer herbivores a lower predation risk (Murray & Illius, 2000) or higher nutrition or palatability (Anderson et al., 2010; Archibald, 2008; Kerby, Fuhlendorf & Engle, 2007). Incorporating these mechanisms into the influence of pyric-herbivory is difficult due to lack of research and a high number of variables which have to be considered (Archibald, 2008).

The response of prey to predation is a central issue in ecosystem ecology with predation not only influencing prey species but subsequently landscape characteristics (Hairston et al., 1960). Changes in herbivore population numbers and spatial concentration due to the presence of predators can influence plant community structure by altering where herbivores concentrate their feeding (Gude et al., 2006). The need for herbivores to balance safety while still meeting nutritional requirements influences their distribution within a landscape (Ripple & Beschta, 2006).

The structure of plant communities, movement of prey and predator species, utilization of burnt areas by herbivores is driven by trophic cascades. Trophic cascades occurring from an upper to a lower level are described as top-down while tropic cascades from a lower to an upper level are described as bottom-up (Hunter & Price, 1992; Scholes, Bond & Eckhardt, 2003). It has been widely disputed whether bottom-up or top-down factors determine the structure of communities. Plant communities are driven by bottom-up factors (geology, soil moisture etc.) on a large landscape scale and by top-down factors (herbivory, parasites etc.) on a fine local scale. Animal communities are driven by a combination of both bottom-up (resource availability and heterogeneity) and top-down factors (predation) of which the relative importance of each varies from species to species (Hunter & Price, 1992; Anderson et al., 2010). Understanding why and how herbivores choose their habitats is important because it helps us to understand what sorts of landscapes and fire regimes will promote different types of herbivores. It also aids in explaining herbivore distributions spatially and herbivore population dynamics over time. This knowledge aids with conserving all herbivores, including rare/engendered species (Owen-Smith et al., 2012), as well as promoting discussions and making practical suggestions on how to apply fires in conservation areas. Current fire management practices do not consider feedbacks to herbivores and focus mostly on large-scale vegetation structure. This might inadvertently have resulted in less herbivore-friendly environments in Kruger National Park and other conservation areas (Archibald 2005). This research is therefore an important contribution to a more systemic management of fire and herbivory in our conservation areas.

1.2 Aims and Objectives

In general it is clear that both fear of predation and a need for forage affect herbivore habitat choice. Although it has been shown that herbivores utilise post-fire burn areas (Tomor & Owen-Smith, 2002; Wilsey, 1996), it is not clear whether they are utilising them for the increased visibility and protection from predators that they offer, or for the high-quality forage. This is due to some studies occurring in areas where no predators where present (Masse & Cote, 2009). It is likely that the relative importance of these two drivers depends on the herbivore type (Sensenig et al., 2003): hind-gut fermenters and fore-gut fermenters have different forage needs, as do large and small-bodied grazers. Large-bodied animals and small-bodied animals are also differentially vulnerable to predators, and this is also affected by their social structure. Predator type also plays an important role, with herbivores reacting differently to stalking and perusing predators (Hayward & Kerley, 2005).

I designed an experiment to test the relative importance of resources and the landscape of fear in driving herbivore use of burned areas in the Satara region of the Kruger National Park. I used variation in fire size and fire season to produce different post-fire resource and predator environments. The first objective of this thesis was to compare forage availability and the landscape of fear across these treatments to quantify the changes in resources and fear of predation offered by different post-burn environments. The second objective was to look at how different herbivores responded to the burn treatments, to determine whether resources or fear of predation were driving their habitat choice.

This thesis consists of an introduction Chapter (Chapter 1) and a Chapter with detailed explanation of the study area, experimental design and methodology (Chapter 2). Two result chapters investigate: 1. the impact of different fire sizes and seasons on forage resources and fear of predation (Chapter 3), 2. the preference of different herbivores for these post-burn environments to determine the relative importance of these two drivers (Chapter 4). Each result Chapter has its own introduction as well as objectives and predictions. A conclusion Chapter (Chapter 5) summaries the findings of the thesis.

2 CHAPTER 2: DESCRIPTION OF STUDY AREA

2.1 Study site

The study site is located in the Satara region of the 1 984 200 ha Kruger National Park, South Africa (S 24^0 23.697', E $31^0$46.577') (Figure 2.1). The area is described as a summer rainfall region, falling into the lowveld bushveld climatic zone, with a mean annual precipitation of 500-700 mm (Gertenbach, 1983; Venter et al., 2003; Rutherford et al., 2006), which is concentrated from October to April (Venter et al., 2003). Temperatures range from approximately 34 °C maximum in January to 9 °C minimum in June, with a mean annual temperature of 21.7 °C during the day (Venter et al., 2003; Rutherford et al., 2006). Humidity ranges from 50-53 % in summer and 37-42 % in winter (Venter et al., 2003).

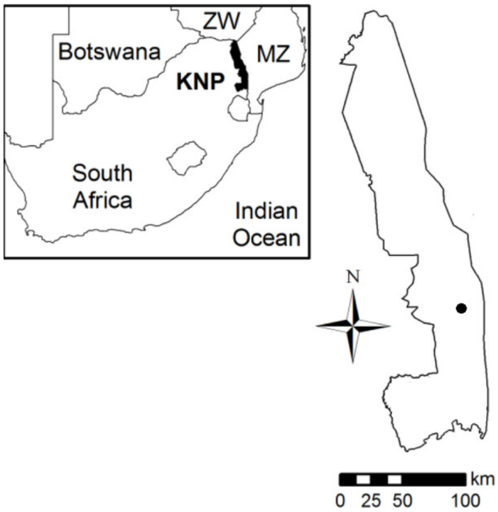


Figure 2.1 Map of Kruger National Park in South Africa (Colgan et al., 2012)

Figure 2.2 Satara landscape June 2013

The Satara area is characterised by two main vegetation types, namely Tshokwane-Hlane Basalt Lowveld, which is the dominant vegetation type within the study site, and Delagoa Lowveld which occurs southwest of Satara (Rutherford et al., 2006). Gertenbach (1983) describes the vegetation type as *Sclerocarya birrea/Acacia nigrescens* savanna. The landscape consists of fairly flat plains (Venter et al., 2003) with well defined drainage channels and a moderately developed shrub layer and open tree savannas (Gertenbach, 1983; Rutherford et al., 2006) (Figure 2.2). Other important tree and shrub taxa include *Combretum hereroense*, *C. imberbe*, *Dichrostachys cinerea*, *Gymnosporia maranguensis* and *Peltophorum africanum*. The dominant grass species occurring in the study site include *Aristida congesta, Bothriochloa radicans, Cenchrus cilaris, Chloris virgata, Digitaria eriantha,* *Enneapogon cenchrodies, Eragrostis racemosa, Eragrostis superba, Panicum coloratum, Panicum maximum, Schmidtia pappophoroides Setaria incrassata, Themeda triandra, Tragus berteronianus* and *Urochloa mossambicensis* (Rutherford et al., 2006).

The study site is dominated by the Letaba Formation Basalts from the Karoo Supergroup (Venter et al., 2003). Soils vary from black, brown or red clayey and are, on average, no more than 1m in depth (Rutherford et al., 2006). Gertenbach (1983) describes the soil pattern as being 'relatively homogeneous'.

The area around Satara is described as Kruger National Parks centre of blue wildebeest (*Connochaetes taurinus)* and Burchell's zebra (*Equus quagga*) habitat (Gertenbach, 1983). Other faunal species present in the study site include buffalo (*Syncerus caffer*), cheetah (*Acinonyx jubatus*), elephant (*Loxodonta africana*), giraffe (*Giraffe camelopardalis*), impala (*Aepyceros melampus*), kudu (*Tragelaphus strepsiceros*), leopard (*Panthera pardus*), lion (*Panthero leo*), steenbok (*Raphicerus campestris*), spotted hyena (*Crocuta crocuta*), waterbuck (*Kobus ellipsiprymnus*), warthog (*Phancochoerus aethiopicus*), white rhino (*Ceratotherium simum*), and occasionally, wild dog (*Lycaon pictus*).

Figure 2.3 Common faunal species of the Satara region in Kruger National Park, impala (*Aepyceros melampus*), *blue wildebeest (Connochaetes taurinus) & Burchell's zebra (Equus quagga).*

Management in Kruger National Park practiced prescribed burning regimes for approximately 36 years until 1992 when concerns were raised regarding the current fire management. After this, a policy for natural fires was adopted where anthropogenic fires were suppressed and lighting fires allowed to burn. From 2002 the fire management policy changed again with patch burning, lightning ignitions and suppression of fires in areas where they were not considered natural (Van Wilgen et al., 2003).

2.2 Experimental design

This experimental design aims to test how the application of different fire sizes, during different seasons, affects the landscape of fear and resource quality, and how this, in turn, influences site selection by herbivores under post-fire conditions. The experiment was located within two of the fire management blocks used by Kruger National Park management (Appendix 1). Management blocks are created when the landscape is divided into sections with natural or anthropogenic boundaries such as rivers and roads. Management blocks were used to apply management fires in the past. Traditional fully factorial experiments are very difficult to apply at landscape scales due to external factors which occur at both a fine and coarse scale (Odum & Jordan, 1970).

The experiment was designed to include two different fire season treatments (early dry season/EDS in May and late dry season/LDS in September/October), three different fire treatment sizes (0.25 ha (50 m x 50 m), 5 ha (220 m x 220 m) and 25 ha (500 m x 500 m)). Each treatment was planned to be replicated four times with four control plots matching the largest treatment plot (ie. 25 ha). However, due to lack of physical space in the landscape and a high fuel moisture content, I was only able to apply two of the three fire sizes for the EDS (0.25 ha and 5 ha). Also, due to extreme weather conditions, I was only able to burn two 25 ha replica plots instead of four during LDS. The fire escaped on one of the 25 ha plots in 2013 and consequently ended up with a 25 ha and a 44 ha burn (Figure 2.4A) and due to a low fuel load only three 5 ha replica burns were able to be applied.

Table 2.1 Sample size (n) for all fire treatment sizes and controls for both EDS and LDS. The four control plots were used as controls for both fire season treatments.

Plot	**EDS sample size (n)**	**LDS sample size (n)**
0.25 ha	4	4
5 ha	4	3
25 ha	0	2
Control (25 ha)	4	4
Total n	**12**	**13**

Fire experiments can be notoriously difficult to manage due to unplanned fires. Management fires and natural fires were meant to be excluded from the fire management block and suppressed across surrounding management blocks for the duration of the research. However a natural fire burnt through the North East corner of the study site in July 2013 leading to the relocation of two treatment plots.

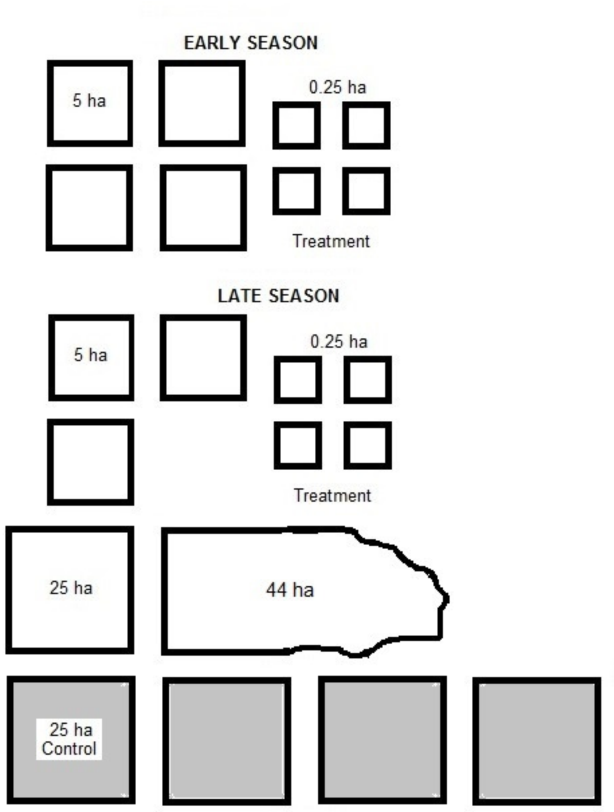


Figure 2.4A Graphic representation of fire treatment size classes and controls for both early and late dry season applications.

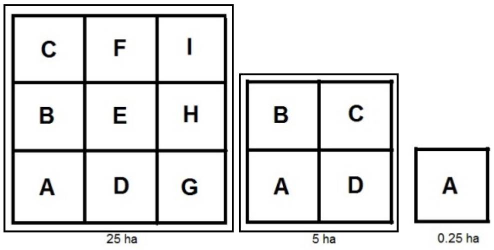


Figure 2.4B Division of plots into subplots.

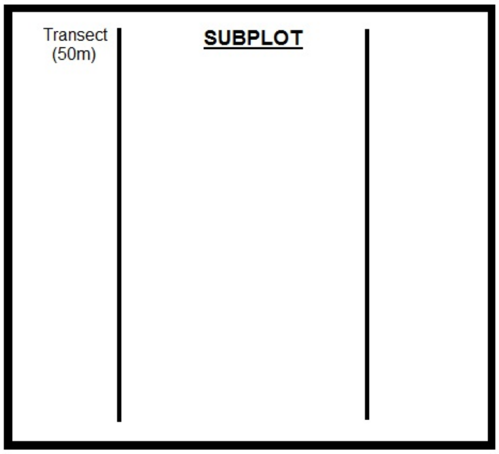


Figure 2.4C Description of a subplot with two 50 m transects.

Due to the range of plot sizes in this experiment, I had to increase the sampling effort on the larger plots to ensure that the variability in these plots was adequately represented. To do this I created a minimum sampling “subplot” (Figure 2.4B) which fitted into a 50 m by 50 m square plot. Two 50 m transects, were located within each sampling subplot (Figure 2.4C). Each transect was marked at the start and end points with 1.2 m steel droppers and pink tape. On the 0.25 ha burns one of these sampling subplots filled the whole plot, on the 5ha burn I placed four subplots and nine subplots were placed on the 25 ha burns (evenly spaced throughout the burn blocks). The controls consisted of four 25 ha plots with nine subplots each, and these were used for comparison for both EDS, LDS and all size classes. Results from all subplots within a burn plot were averaged and used as a single replicate for statistical analyses. In this thesis 0.25 ha plots are labelled as 0.25, 5 ha as 5, 25 ha as 25 and control plots as 25C.

2.3 Data collection frequency

Data collected included grass height, grass biomass, grass greenness, grass samples, dung counts, animal observations and camera traps. Data were collected one month before fire treatments were applied and at repeated intervals following the fire to reflect change over time (Figure 2.5). EDS pre-fire sampling was conducted in April, two weeks prior to the initiation of the burn treatments at the end of April. Six post-fire re-sampling visits were conducted in May, June, July, November, December 2013 and January 2014. EDS had a total of 36 transects for all treatment plots per sampling period, totalling 252 transects over the duration of the study period.

LDS pre-fire sampling was conducted in August and plots were burnt in October. Three post-fire re-sampling visits were conducted in October, November 2013 and January 2014. LDS had a total of 68 transects for all treatment plots per sampling period, totalling 272 transects over the duration of the study period.EDS and LDS both had a total of 72 transects per sampling period for controls, totalling 504 transects for EDS and 288 transects for LDS over the duration of the sampling period.

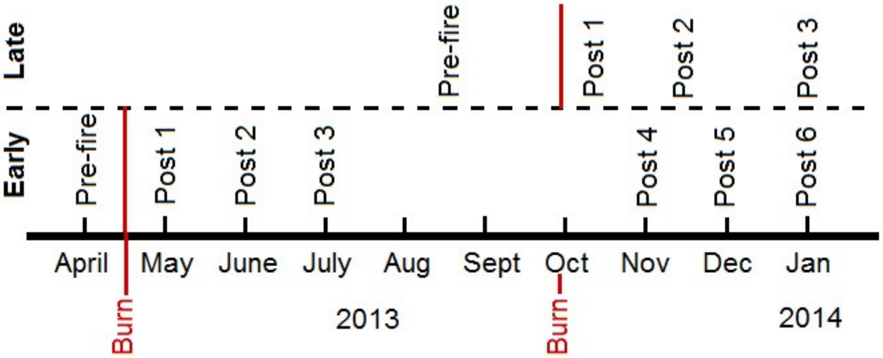


Figure 2.5 Data collection intervals for all treatment and control plots.

2.4 Data collection methodologies

Data collection methodologies for all chapters are described below and are arranged in rough categories (example: grass height, biomass and greenness) and in order of result chapters. All data collected below was measured on all plot sizes, treatments and controls. Comparisons were made between both early and late dry season as well as controls and treatments to show change over time and compared to the landscape.

Percentage of transect burnt was recorded immediately post-fire in order to determine the 'completeness' or 'grain' of burns for both EDS and LDS fires (Sensenig, Demment & Laca, 2010). The percentage of each transect that burned was quantified by walking the transects and recording length (m) of burned patches. These transect data were summed to determine the percentage of each plot that burned. Percentage of transect burnt provides an indication of the difference in visibility/vegetation structure and thus perceived predation risk between EDS and LDS burns.

Vegetation structure is used to indicate perceived predation risk in regards to predator avoidance or herbivore escape behaviour (Wirsing, Cameron & Heithaus, 2010).Vegetation structure was quantified at two points along each 50 m transect. Vegetation structure was recorded at four heights (0.3 m, 0.5 m, 1 m and 1.5 m) in two directions perpendicular to the transect line. These heights represent the eye height of three herbivore species Burchell's zebra (*Equus quagga)* blue wildebeest (*Connochaetes taurinus*), impala (*Aepyceros melampus*)) with head down and with head raised above shoulders respectively. It was decided to use 0.3 m as an accurate height to represent the head down position (when feeding), and 1.0 m as an accurate height to represent the head raised position (when walking/vigilant) for all three species. An A4 white board was carried away from the transect in two directions at the respective heights and viewed from the transect at the same corresponding height. Once 50 % of the board had been obstructed the distance between the board and the transect was recorded (up to a maximum of 20 m).

Grass height and biomass were collected monthly at 5 m intervals along each 50 m transect. Total grass height was measured using a 2 m pole marked out in 5 cm intervals using the tallest leaf. Grass biomass was measured using a disc pasture meter (Trollope & Potgieter, 2007).

Grass quality (nitrogen) was assessed by sampling at 5 m intervals along each 50 m transect. A small handful of grass leaves was randomly picked and stored in paper bags as a representative bite of a non-selective grazer. The two transects' samples were then pooled to produce one grass sample per subplot in order to determine total Nitrogen (Van der Waal et al., 2011). The grass samples were dried in a drying oven at 60-65 ^{0}C for 48-72 hours, after which they were ground and passed through a 1mm sieve before being stored in ziplock bags. Each ziplock sample contained approximately 20 g of dried grass. Total Nitrogen was determined using the Kjeldahl method (Nelson & Sommers, 1973; Agrilasa, 2002; Helrich, 1990). The Kjeldahl method measures percentage ammonium (NH_4) and expresses this result as a percentage per sample. There are no methods which can satisfactory determine total Nitrogen (N) as each method will have an effect on a structural component of the plant sample and in some way degrade sugar or protein molecules (Rranker, 1925; Nathan & Sun, 2006).

Grass greenness was estimated monthly at 5 m intervals along each 50 m transect at the same points where biomass was measured. The percent of the sward under the disc that was green was assessed by using the following simple categories: <25 %, 25-50 %, 50-75 %, >75 %.

Tree density in each subplot is measured using a Bitterlich-wedge and is recorded once. The wedge consists of a 50 cm rope with one end attached to a metal block consisting of four different sized slits (0.25 cm, 0.5 cm, 0.75 cm and 1 cm), one on each side of the block. Size class 0.25 cm was selected for the study site. The number of trunks or stems that were larger or equal to the selected size class were counted by viewing the trunks through the slit at eye-level and rotating 360 degrees. The final count is multiplied by 0.25 in order to determine the biomass of trees in square meters per hectare. Tree density provides an indication of visibility and perceived predation risk.

Grass species composition was conducted on a broad scale by recording every grass or forb species along each 50 m transect at eleven points twice during the study period (pre and post-fire). Forbs were classified as either non-leguminous forbs or leguminous forbs based on their leaf structure. The number of forbs per transect were added and a percentage of forbs per plot was achieved for both pre-fire conditions and post-fire conditions. The mean of this percentage forbs was then calculated using these two measures.

Distance to water was calculated by measuring from the centre of the plot to the nearest source of water using Google maps. These distances are estimations and have been recorded in kilometres. Tree density, forb percentage (under pre-fire conditions) and distance to water were compared to mean pre-fire dung counts for all three herbivore species (impala, blue wildebeest and Burchells zebra) using a Pearsons correlation.

Dung counts were used as a proxy to determine which species were using plots. All dung within 2 m of each side of the 50 m transect (4 m x 50 m belt transect) was recorded by species. Counted dung piles were squashed or spray-painted to prevent recounts. Dung counts were validated against animal observations and data from camera traps to provide an indication of plot use (Archibald, 2005; Van der Waal et al., 2011).

Dung presence was assessed on all sampling transects once a month. EDS treatment plot transects were sampled 7 times from April 2013 to January 2014. LDS treatment plot transects were sampled four times from August 2013 to January 2014.

In addition to dung counts, animals observed using the plots were recorded during specific observation periods. The roads through the study site were driven at different times to ensure temporal heterogeneity throughout the day and each plot visited at least three times a week. Animal observations were limited by other field work, tourist pressure (disturbances during observations) and Satara gate opening and closing times. Observations were done from a vehicle. For each plot I either recorded no animals present, or where animals were present I recorded the distance of the animals using a rangefinder. For each sighting the following were recorded: the species, number of individuals, number of groups, number of animals on and off the plot, distance between groups, distance between individuals within each group, distance of the individual in the centre of the group to the plot edge and the distance of the individual closest to the group edge to the plot edge. Animal behaviour was also recorded. Two scans were conducted on each animal group with five minutes between scans. For each scan the activity of each individual was recorded. Behavioural activities were: vigilant (head up, ears alert), walking, grazing, browsing, grooming and lying down/resting. Time, approximately five minutes, was given for animals to return to normal behaviour after a disturbance (i.e. car passing).

EZ-CAM camera traps with external 12V batteries as a power source, were used to document the use of plots by animals pre- and post-fire. Due to logistical constraints limited EDS pre-fire data were collected. The cameras were triggered by movement and took photos in sequences of three, after which the camera took 1 minute to reset. The cameras were dispersed between controls and treatments. I didn’t have enough cameras to sample EDS and LDS plots concurrently, so the observations on the EDS plots were limited to April 2013-October 2013, after which the cameras monitored the LDS plots until April 2014. When a photograph picked up herbivore presence I recorded the species and whether it was day or night. The number of days that the camera was active on each plot was also recorded. From this the number of pictures/day/species and number of pictures/night/species was calculated by determining the number of day/night photographs per species and dividing it by the total amount of time the camera was active. This was done in order to determine the dominant herbivore users of the plot and to compare with data from dung counts.

3 CHAPTER 3: EFFECTS OF FIRE ON THE LANDSCAPE OF FEAR AND FOOD

3.1 Introduction

The effect fire has on vegetation is highly variable due to many factors including weather conditions, ignition sources (Tainton & Hardy, 1999), fuel availability and fuel arrangement temporally and spatially (Trollope, Trollope & Hartnett, 2002), the presence of herbivores and previous disturbances (Archibald et al., 2009; Rutherford et al., 2006). Fuel load is determined by rainfall, tree density and grazing pressure. Fuel moisture and thus fuel flammability is determined by rainfall and the length of the dry season (how long fuel has been given to cure) (Govender et al., 2006; Archibald et al., 2009). Fuel continuity is determined by topography, grazing and barriers (natural or man-made) (Hoffman et al., 2012; Kreye et al., 2013). Wind speed combined with fuel properties influence fire intensity (how hot the fire is), spread (how fast it can spread) and thus the size of the subsequent burn (Archibald et al., 2009). Fire behaviour and spread influences patterns of burnt and un-burnt areas. These patches of burn feedback into patch selection by herbivores (Kerby et al., 2007; Trollope, Trollope & Hartnett, 2002). Season has an effect on fuel moisture content influencing fire intensity, which is low when fuel moisture content is high and high when fuel moisture content is low (Govender et al., 2006), thus fire season has an impact of fire behaviour and spread.

Late dry season (LDS) fires generally occur between July and October in the Kruger National Park and are described as “moderate to high-intensity” fires (Van Wilgen et al., 2014) and are considered the norm for removing moribund material. Historically LDS fires were only set after the first rain in order to ensure that the growth of the grass was not hampered. Fires set outside of the LDS were used to create an out of season green-flush and were mainly employed by the agricultural industry or as a management tool (fire breaks) (Sow et al., 2013; Trollope et al., 1990). Early dry season fires (EDS), generally occurring between February and May and described as mild intensity fires, have been used to mitigate potential LDS fires, however the incorrect application of EDS fires can be detrimental to vegetation (Sow et al., 2013). This being said, burning under different fire regimes promotes landscape heterogeneity and biodiversity (Van Wilgen et al., 2014, Brockett et al., 2001).

Dormancy in plants is an ecological adaptation to environmental change and disturbances and is defined as a “temporary suspension of visible growth of any plant structure containing a meristem” and is furthermore it is described as a “stationary phase” in plant production. Seasonal environmental changes lead to changes in available resource which are necessary to maintain plant growth. During resource scarce times plants can become dormant in order to conserve resource until more favourable conditions arise in which they can grow (Volaire & Norton, 2006).

The season that fire occurs also affects how and when grasses re-grow: during the dry season grass growth is limited by water availability (Georgiadis et al., 1989). Fires occur more frequently and intensely during this season due to low fuel moisture and high fuel biomass (Govender et al., 2006). During the wet season water availability is not limited and grasses are in a growth phase where resources are being used to grow and are no longer stored (Volaire & Norton, 2006). Burning grasses during their growth phase hampers the grasses ability to re-grow (Belsky, 1992).

In the majority of cases herbivores have been shown to be attracted to post-fire vegetation (Klop et al., 2007; McNaughton, 1983; Moe & Wegge, 1997; Tomor & Owen-Smith, 2002; Van de Vijver et al., 1999). There are two main hypothesis for this attraction, change in resources and change in predation risk, however it is poorly understood to which extent herbivores are driven by these two factors (Burkepile et al., 2013; Riginos & Grace, 2008). Other possibilities for this attraction include reduction in tick load (Spickett et al., 1992) and access to minerals concentrated in the post fire ash (Dills, 1970; Van de Vijver et al., 1999). By understanding how fire impacts both forage resources, in regards to forage quantity and quality, and predation risk we can try untangle the importance of these two factors and try understand why herbivores respond to these changes.

Van de Vijver et al., (1999) determined that there is an initial increase in grass nutrient concentration (N, P, K, Mg) directly post-fire. In his study grass nutrient concentrations decreased to pre-fire conditions within three month. However we expect the extent and duration of this nutrient concentration post-fire enhancement to depend on various factors including soil nutrient status, amount of burned material, the amount of ash produced and whether grass continued to be grazed or not (Van de Vijver et al., 1999). Grass species composition differs at both landscape and fine scale level. Herbivores have been shown to select grass species based on nutrient content and palatability (Treydte et al., 2013). A study in Kruger National Park by Treydte et al., (2013) showed that *Urochloa mosambicensis* (%Nitrogen = 1.76) and *Panicum maximum* (%Nitrogen = 1.78) were two preferred forage species for a variety of grazers due to their high nutrient content compared to *Aristida* species (%Nitrogen = 0.68), *Digitaria eriantha* (%Nitrigen = 0.92) and *Bothriocloa radicans* (%Nitrogen = 1.24).

Enhanced post-fire nutrient concentration is thought to be due to an increase in leaf: stem ratios. The plants nutrients are thus concentrated in relatively little above ground biomass when the grass is short (shortly post-fire), however as the grass grows the nutrients are spread throughout the increasing above ground biomass (late post-fire) (Van de Vijver et al., 1991). Grass post-fire has a lower lignin content and higher nutrient content than mature grass, thus initial post-fire forage quality is expected to be higher than pre-fire forage quality (Van de Vijver et al., 1991; Van de Vijver et al., 1999). It is then expected that post-fire forage quality will decrease over time to its pre-fire condition unless grazing pressure stimulates constant re-growth, thus maintaining a higher state of forage quality.

Fire affects plant and soil nutrient cycling (Coetzee, 2005), modifies plant diversity and plant species composition as well as causes changes in tree cover and vegetation structure (Eby et al., 2014). By removing moribund material, fire stimulates grass re-growth, also referred to as a green-flush (McNaughton, 1983; Allred et al., 2011). Within burned areas variability in fire intensity and topography leads to differences in grass height and nutrient content, which affect the spatial distribution of forage and its overall quality. Variation in forage quality in turn influences the selection of burned areas by herbivores leading to heterogeneity in habitat use (Klop et al., 2007).

Lima (1992) divides the natural environment into safe and unsafe areas based on risk of predation. Factors contributing to the safety of the environment include tree-density, vegetation structure visibility (Klop et al., 2007; Smit, 2011), group size and number of species (Lima, 1992; Riginos & Grace, 2008). In Hwange National Park, Zimbabwe, Valeix et al., (2009) showed that the distribution of eleven herbivore species (including zebra, wildebeest and impala) were determined by perceived predation risk, where the selection of areas by animals was based on vegetation structure. Vegetation structure plays an important role in determining the foraging behaviour of a species with denser vegetation leading to higher vigilance and reduced foraging time which in turn affects the use of landscapes (Beecham & Farnsworth, 1999; Riginos & Grace, 2008; Smit, 2011).

Fire alters vegetation structure by reducing grass height and knocking back shrubs and saplings (Bond & Keeley, 2005) allowing for a higher visibility (Tolon et al., 2009). Herbivores respond to alterations in the landscape of fear and are attracted to areas which minimize predation (White et al., 2003). Sufficiently sized burnt areas serve as low-risk areas and offer not only higher visibility but a potential increase in resource (Tolon et al., 2009). Tolon et al., (2009) suggests that animals have a threshold distance, beyond which they do not respond to changes in the landscape of fear. Size of burn can therefore influence a herbivores escape behaviour/vigilance in regards to visibility (Allred et al., 2011) and flight distance (Wirsing, Cameron & Heithaus, 2010). Theoretically, if each plot size in the study area was burnt cleanly, from the centre of each plot 0.25 ha plots would have a flight distance of 25 m, 5 ha a flight distance of 110 m and 25 ha a flight distance of 250 m.

The variation in ecological landscapes leads to a high variability in resources and variability in herbivore usage of the landscapes. Topography, distance to water, forage quality and quantity, and perceived and real fear of predation all affect herbivore use of a landscape, which means that when trying to assess the role of one factor it is important to be aware of and try to control for other factors. (Redfern et al., 2003). (Bailey et al., 1996; Redfern et al., 2003). The extent to which burned areas are selected by herbivores is influenced by distance to water, vegetation cover and topography (Klop et al., 2007), as well as the intrinsic attractiveness of the post-burn landscape.

Seasonal changes in water availability determine the dependence of animals on water resources and thus the use of the landscape (Smit, 2011). Distance from water impacts herbivory, this is demonstrated around water points where grass closer to the water source is intensely grazed and thus shorter than grass further away from water sources which are less-intensely grazed and taller (Fornara & Du Toit, 2008). During the dry season herbivore distribution is restricted by water availability, where as in the wet season, temporary water sources allow for a larger spatial distribution of herbivores (Smit, 2011).

Forbs have been found to be highly digestible and have a higher nutritional value than many other grasses and woody plants (Everitt et al., 1999; Owen-Smith, 2002). They are considered as “one of the most important plant groups for herbivores” (Everitt et al., 1999). Forbs usually occur in the early succession stages after a disturbance and usually occur in minority, however their nutritional value makes them highly sought after by various herbivores as a supplement (Cherney & Cherney, 2004; Owen-Smith, 2002). Selective grazers have been noted to select forbs when available as they are more focused on forage quality than quantity (Sensing et al., 2010).

Tree density and structure is the outcome of a number of variables: geology, topography, soil moisture, and past and present disturbance history (Levick et al., 2012). Although woody structure is strongly driven by fire and herbivory, (Shackleton & Scholes, 2000; Ekblom & Gillson, 2010) it also impacts the occurrence of these disturbances through impacting the composition and biomass of the herbaceous layer (Riginos & Grace, 2008; Ekblom & Gillson 2010; Hoffmann, 2012).

In regards to predation risk, higher tree-densities are associated with decreased visibility and thus a decreased predator detection. High tree densities have been show to increase herbivore vigilance which negatively impacts forage intake (Riginos & Grace, 2008). Tree density not only influences vegetation structure and visibility but has been found to influence forage quality of understory grasses (Treydte et al., 2011). Tress can be considered as islands of fertility with elevated soil nutrients and different light and water characteristics than open areas. Treydte et al (2011) states that various ungulate species including impala, zebra and blue wildebeest, prefer understory grasses. Understory grasses can allow for a build up of reserves for selective grazers to carry them through the dry months due to a variation in quality when compared to open grass areas (Treydte et al., 2011). However, if trees get too thick then the grassy understory disappears entirely, and the forage for grazing animals declines (Coetzee, 2005).

3.2 Aims and Objectives

This chapter aims to document post-fire environment in terms of the landscape of fear (visibility) and resource (forage) quality and quantity and how and if it changes over time with regards to different fire season (EDS and LDS) and fire size. Higher level environmental factors can influence the results and that these factors can be used to explain why herbivores have preferences to areas which are less suitable in regards to predation risk or forage.

These data will then be used in Chapter 4 to determine how herbivores respond to these changes, and whether resource (bottom-up) or fear of predators (top- down) is driving their habitat choice.

In this chapter the following hypothesis will be tested:

- Fire season impacts percentage of transect burnt. EDS burns will be more patchy or discontinuous than LDS burns which will be continuous, due to differences in fuel moisture.
- Visibility will increase after the fires in both EDS and LDS burns, but more in LDS burns due to LDS burns having a cleaner, less patchy burn than in EDS.
- Grass height influences visibility at different animal head heights. Grass height has a greater influence on visibility when an animal is in the head-down position compared to the head-raised position.
- Fire size affects the overall quantity (biomass) of palatable forage because the larger the area burnt the higher quantity of grass re-growth.
- Post-fire forage quality (total nitrogen) will be higher than pre-fire forage quality for both EDS and LDS burns, and this will decrease with grass height as the grass re-grows.
- Forage production depends on rainfall, so after the first green flush burn sites will not continue to produce more biomass until the rains arrive (i.e. forage quantity will remain low on the EDS burn sites).

- There is no significant variation in distribution of environmental factors and thus they do not have a confounding affect on results.

3.3 Data Analysis

Percentage transect burnt data was analysed using a Mann-Whitney U test and a Kolmogorov-Smirnov test. The length of burnt and un-burnt patches for both transects was summed in order to determine the percentage of plot burnt. Confidence intervals were determined to demonstrate variability in the data. Comparisons were made between EDS and LDS as well as plot size. Visibility (m) and forage quantity data (biomass in kg/ha) were averaged per plot replicate and analysed using Analysis of Variance (ANOVA) and Tukey HSD in order to determine whether they differed significantly among sampling periods, seasons and plot sizes.

Visibility was compared to total average grass height using a Pearsons correlation at all four height classes to determine which of the head down height classes (0.3 m or 0.5 m) and head up height classes (1.0 m, 1.5 m) showed the most significant correlation. Once these two heights were determined, change in visibility for EDS, LDS and controls were compared to determine changes overtime using a Repeated Measures ANOVA. Change in grass height over time for EDS, LDS and controls was also determined separately using a Repeated Measures ANOVA in order to support both visibility as well percentage transect burnt data.

Biomass (kg/ha) was used as a measure of resource quantity. The mean biomass over time was calculated for EDS, LDS and controls using a Repeated Measures Analysis of Variance. Percentage greenness data were converted from categorical percentage data to a mean percentage greenness per plot replicate by determining the midpoint of each category (<25 % = 12.5, 25-50 %= 37.5, 50-75 % = 62.50, >75 % = 87.5) and counting the frequency that each occurred per subplot. The count for each category was multiplied with each midpoint of the respective category. This total was divided by the sum count of all the categories to determine the mean percentage greenness. Mean percentage greenness was multiplied with mean biomass data in order to determine mean green biomass (kg/ha) and thus possible edible biomass over time. Percentage greenness data were analysed using an univariate Analysis of Variance (ANOVA) and Tukey HSD. Total biomass per plot size and total green biomass (and their respective standard deviation) was calculated for three sampling periods and tabulated in order to show changes over plot size and time for both seasons and the control.

Grass sample analysis results were converted from percentage NH_4 into total N (mg/l) by multiplying by ten (Helrich, 1990; Nathan & Sun, 2006). These data were analysed using a Repeated Measures Analysis of Variance. Grass greenness and total N data were compared on a subplot level in order to represent the differences or correlation in the data more accurately. All other data sets were compared at a plot size level. This was to determine if grass greenness was indeed an accurate representation of total N. A multiple linear regression model was conducted comparing both grass height and grass greenness to grass N in order to determine which factors are most important in driving nitrogen content. The relationship between grass greenness and grass height and total N content was addressed using a generalised linear model (with probit link) because the data ranged between 1-100. Histograms showing the distribution of each environmental factor were generated and basic statistics were conducted.

3.4 Results

3.4.1 Percentage transect burnt

As predicted, EDS burns were more patchy than LDS burns. The median percentage transect burned in the EDS was 75 (Confidence intervals 25 and 75: 57.7-86.8), compared to 97 (Confidence intervals 25 and 75: 83.8-100) for LDS (Figure 3.1). EDS treatment plots (A) showed a higher variability in percentage transect burnt (K-S d = 0.21532, $p>20$) than LDS treatment plots (B) (K-S d=0.23367, $p<0.05$) (Figure 3.1). Although there was no significant difference in the total percentage transect burnt, for both EDS and LDS the larger plots had a higher variability (Figure 3.2). The LDS 0.25 ha plot however is an exception due to one of the four replicates having higher percentage forbs. Thus when LDS burns were applied the fuel layer on the 0.25 ha plot was discontinuous leading to a higher variability percentage of transect burnt.

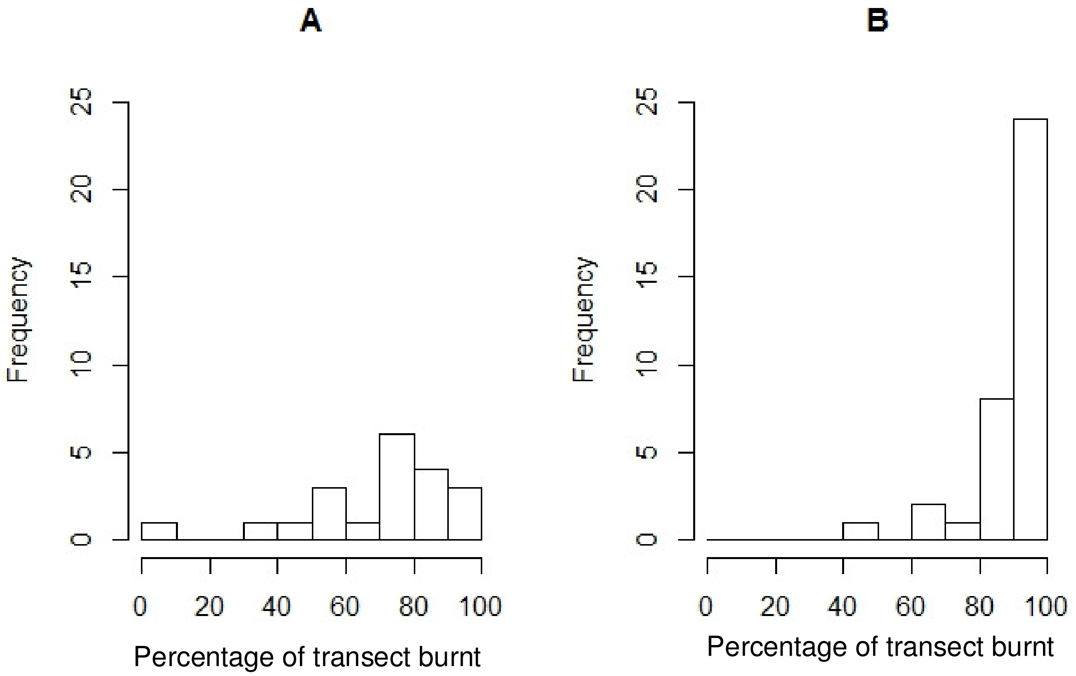


Figure 3.1 Percentage of transect burnt for EDS treatment plots (A) and LDS treatment plots (B), regardless of fire size.

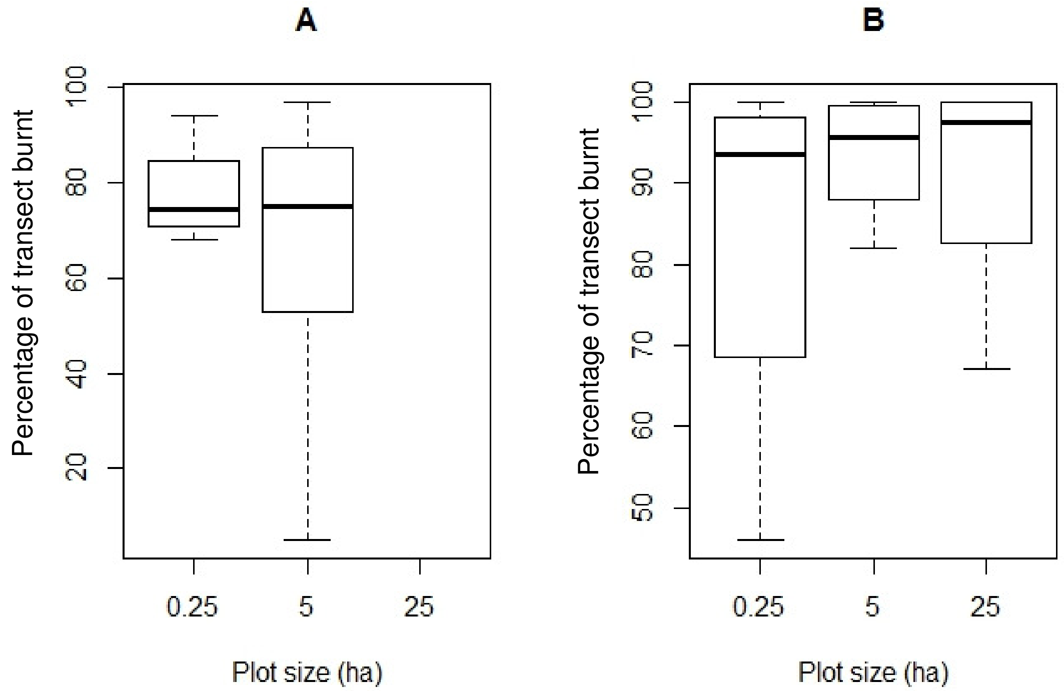


Figure 3.2 Percentage of transect burnt for (A) EDS and (B) LDS for different plot sizes.

3.4.2 Visibility

Visibility versus grass height

Visibility in the head down position (0.3 m (Figure 3.3A) (Pearson's r= -0.707) and 0.5 m (Figure 3.3B) (r= -0.828)) is highest when grass height is below 15 cm, there after visibility decreases to less than 5 m as grass height increases. Visibility in the head up position (1.0 m (Figure 3.3C) (r= -0.582) and 1.5 m (Figure 3.3D) (r= -0.342)) is greater than 15 m regardless of grass height, with 1.5 m height class being the least influenced by grass height. .

Assuming that an animal requires at least 5 m visibility before they feel safe to graze (Ford et al., 2014) the grass height would have to be less than ~17 cm in the head down (0.3 m) position, and less than 40 cm in the 0.5 m position. Visibility is always more than 5 m in the two head up positions (1.0 m and 1.5 m).

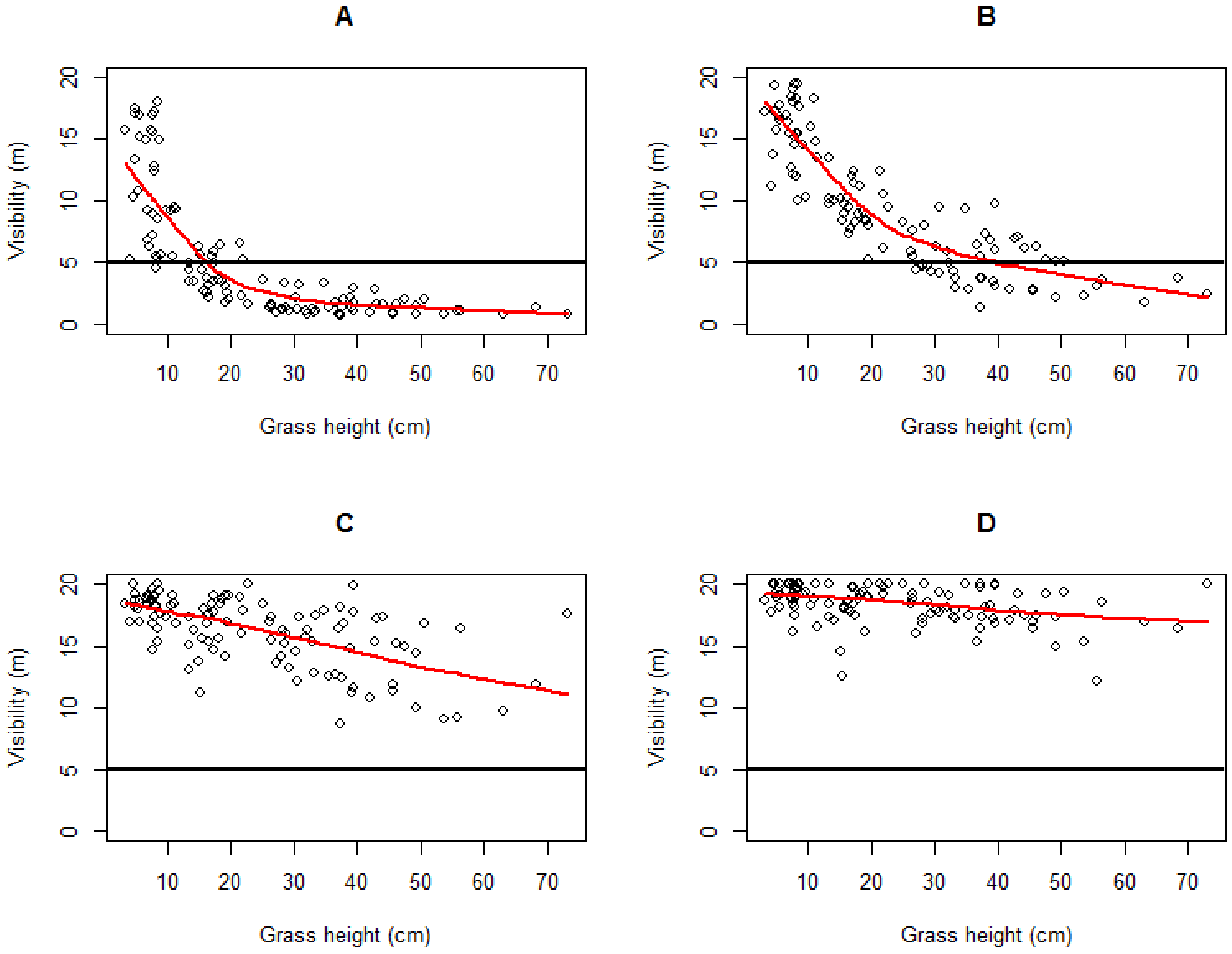


Figure 3.3 Correlation between grass height and visibility at four height classes, 0.3 m (A), 0.5 m (B), 1.0 m (C) and 1.5 m (D). The horizontal black line indicates where the data intersect a hypothesised 5 m flight distance.

Change in visibility over time per season of burn

Visibility on control plots (i.e. un-burnt) remained relatively stable showing no significant differences over time for both 0.3 m (Wilks = 0.76, F(16, 44) = 0.40, p = 0.98) and 1.0 m (Wilks = 0.45, F(16, 44) = 1.35, p = 0.21) height class (Figure 3.4A & 3.4B), but overall visability was much lower than on EDS and LDS burn plots. For EDS sampling period had a significant impact on visibility at 0.3 m height class (Wilks = 0.35, F(8, 68) = 5.97, p = 0.00) with visibility increasing significantly immediately post-fire in May (p=0.00) until July where it significantly decreased in December (p=0.00). Visibility under post-fire December conditions was higher than pre-fire April conditions, however not significantly so. For LDS sampling period had a significant impact on visibility at the height class (Wilks = 0.17, F(6, 62) = 14.65, p = 0.00). As with EDS, there was a significant increase immediately post-fire (p=0.00). From October to November visibility did not significantly change (p=0.83) and started significantly decreasing from November to January (p=0.00). The change in visibility is much more pronounced in the LDS (mean 14 vs. 8m), but within three months visibility had returned to pre-fire levels (Figure 3.4A).

At an observation height of 1.0 m, the effect of burning on visibility was insignificant and much less pronounced than at an observation height of 0.3 m for both EDS (Wilks = 0.65, F(8, 68) = 2.00, p = 0.06) and LDS (Wilks = 0.86, F(6, 62) = 0.82, p = 0.56). Again, visibility increased post-fire in both seasons (Figure 3.4B), although levels of visibility were similar on EDS and LDS burns (approx. 18m) (EDS: F(4) = 19.96, p = 0.001, LDS: F(3) = 21.32, p = 0.000). Therefore fire affects visibility in the head down position more, and might therefore impact vigilance behaviour. Visibility increased over the dry season on the control plots but this is not significant. By the last sampling data there was no significant difference in visibility for both height classes for both EDS and LDS (p<0.05).

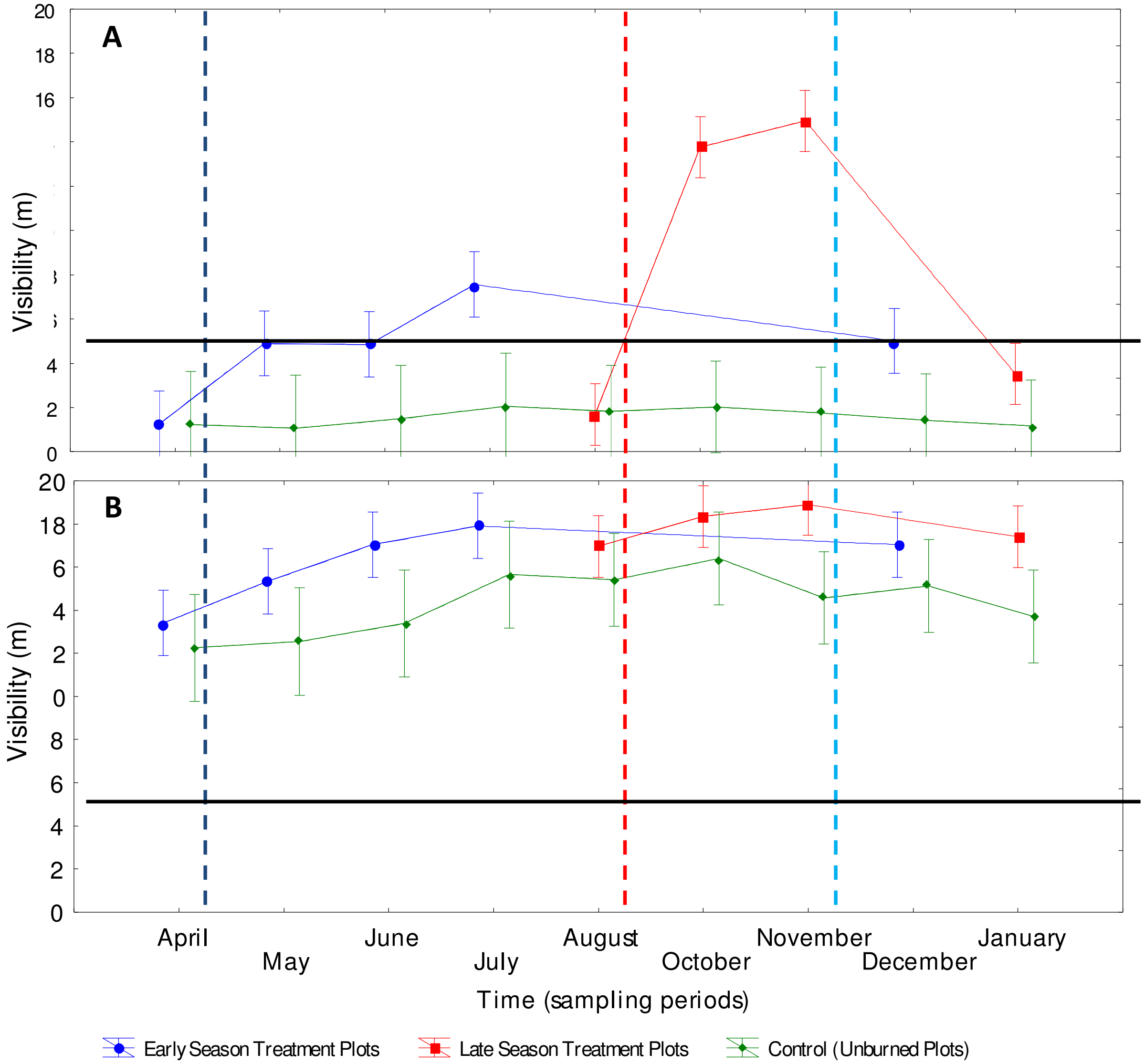


Figure 3.4 Change in visibility over time for EDS, LDS and Controls at height class 0.3m (A) and 1.0m (B). The dotted lines represent burns (EDS = dark blue; LDS = red) and start of rains (Rain = light blue). The horizontal black line indicates where the data intersect a hypothesised 5m flight distance.

3.4.3 Grass Height

Sampling period had a significant impact on grass height on controls (Wilks = 0.86, F(16, 11420) = 56.93, p = 0.00), EDS (Wilks = 0.42, F(14, 5022) = 101.24, p= 0.00) and LDS (Wilks = 0.43, F(6, 6810) = 588.30, p = 0.00). Under pre-fire conditions there was no significant difference between EDS and controls (p = 0.41) and LDS and controls (p = 0.99). Pre-fire grass height of LDS was significantly lower than that of EDS (p= 0.00). Grass height significantly decreased ($p<0.05$) for both EDS and LDS immediately post fire from a mean grass height of 56.59 cm to 16.08 cm and 38.16 cm to 5.17 cm respectively. EDS grass height remained relatively constant from May to November with no significant increase (p>0.05). The increase in grass height after the rains, from November to January was not significant (p= 0.98). LDS grass height started increasing from October to November, however this increase was not significant (p=0.99). At the end of the sampling period (January), both EDS and LDS grass height was significantly lower than pre-fire conditions (p= 0.00).

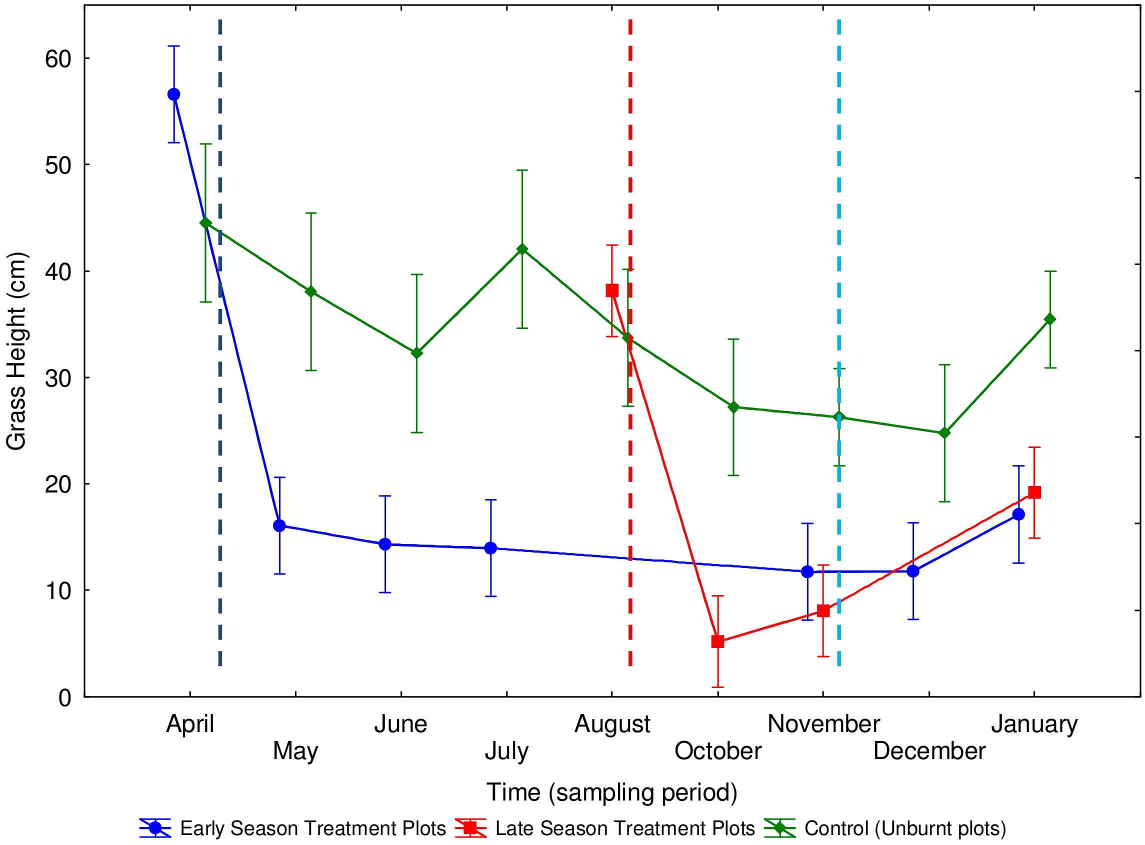


Figure 3.5 Change in grass height (cm) over time for EDS, LDS and Controls. The dotted lines represent burns (EDS = dark blue; LDS = red) and start of rains (Rain = light blue)

3.4.4 Resource quantity

Biomass per season over time

Under pre-fire conditions there was no difference in mean biomass between treatment plots and controls for both EDS and LDS (F(8) = 1.59, p = 0.17) (Figure 3.6A). There was significantly less biomass on both EDS and LDS treatment plots immediately post-fire (p=0.000). Sampling period had a significant effect on biomass of controls (Wilks = 0.08, F(16, 60) = 10.54, p= 0.00), EDS (Wilks = 0.03, F(18, 133) = 16.93, p =0.00) and LDS (Wilks = 0.02, F(9, 73) = 30.29, p= 0.00). For controls biomass in January was significantly higher than December (p= 0.03) and October (p=0.01). On both EDS (April vs January, p = 0.00) and LDS (August vs January, p= 0.00) burn plots, a significantly lower biomass was maintained until the end of the sampling period (which coincides with the end of the growing season).

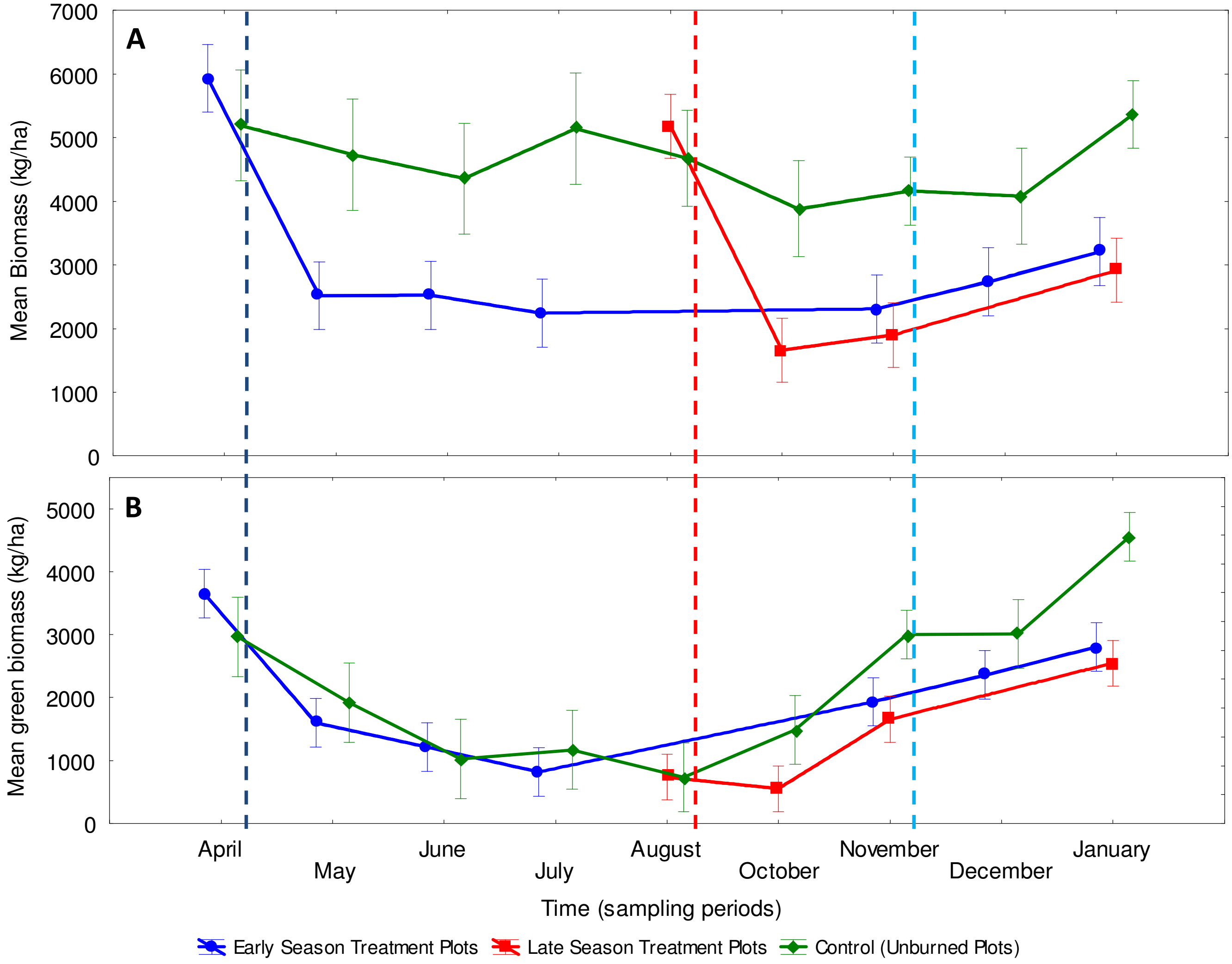


Figure 3.6 Changes of mean biomass (Figure 3.6A) and mean green biomass (Figure 3.6B) over time for treatment plots and controls. The dotted lines represent burns (EDS = dark blue; LDS = red) and start of rains (Rain = light blue).

As will mean biomass, mean uncured (green) biomass was significantly impacted by sampling period in regards to controls (Wilks = 0.01, F(16, 60) = 19.32, p= 0.00), EDS (Wilks = 0.04, F(3, 47) = 358.12, p = 0.00) and LDS (Wilks = 0.04, F(3, 30) = 256.48, p= 0.00). EDS mean uncured (green) biomass (Figure 3.6B) decreased significantly from pre-fire conditions till post-fire July (p= 0.00), after which it increased significantly till post-fire January (p= 0.00). EDS pre-fire April green biomass remained significantly higher than any other sampling period (p<0.05). The LDS mean uncured (green) biomass showed no initial significant increase (August to October, p =0.81). From post-fire October (p= 0.00) till post-fire January there was a significant increase. January mean uncured (green) biomass was significantly higher than August (p= 0.00). Controls mean uncured (green) biomass followed a similar pattern to that of EDS and LDS with uncured biomass decreasing from April till July (p= 0.01)/August (p=0.03) and increasing again till January which was significantly higher than all other sampling periods (p<0.05).

Mean biomass per plot size

As would be expected, there was a higher mean biomass, and green biomass on the larger sized plots overall for both seasons (Table 3.1). Mean green biomass indicates how much of the total biomass in kg/ha was edible and thus how much biomass is available to herbiovires (grass greenness being used as an indication of palatability). Controls consistently had a higher mean biomass than all plot sizes, for both seasons (p<0.000). Under pre-fire conditions (EDS: F(2,44)= 1.84, p= 0.17, LDS: F(3,66)= 1.52, p= 0.22) and last sampling conditions (EDS: F(1,18)= 0.24, P= 0.63, LDS: F(3,52)= 5.75, p= 0.06), there was no significant difference in the mean percentage greenness, with all treatment plots and controls showing similar results for both seasons respectively. Immediately post-fire for the EDS there was however a significant increase in mean percentage greenness of treatment plots compared to controls (F(2,44)= 46.23, p= 0.00). In regards to LDS, only the 25 ha treatment plot showed significantly higher mean percentage greenness than the control (F(3,66) =4.25, p = 0.01).

Table 3.1 Representation of the total biomass, total green biomass per plot (kg) and standard deviation of both in brackets, per season for the following sampling periods; Pre-fire (EDS = April 2014, LDS = August 2014), immediately post-fire (EDS = April 2014, LDS = October 2014), last sampling (EDS & LDS = January 2015).

Season	Plot	Pre-fire		Immediately Post-fire		Last Sampling	
		Total biomass/plot kg (sd)	Total green biomass/plot kg (sd)	Total biomass/plot kg (sd)	Total green biomass/plot kg (sd)	Total biomass/plot kg (sd)	Total green biomass/plot kg (sd)
Early	0.25	6411 (121)	3973 (169)	2515.77 (184.34)	1664 (59)	3239 (294)	2834 (257)
Early	5	109149 (4576)	66712 (3684)	50313 (2097)	30566 (999)	63582 (3772)	55483 (3254)
Early	25C	389442 (25703)	222408 (10872)	355038 (25260)	144038 (10320)	536630 (24006)	455710 (22311)
Late	0.25	5041 (114)	678 (36)	1901 (136)	522 (134)	3102 (273)	2714 (239)
Late	5	81785 (4722)	11656 (442)	24178 (1200)	8097 (2652)	37385 (2181)	32712 (1909)
Late	25	252766 (39300)	39270 (230)	62942 (744)	**31425** **(15936)**	158709 (16490)	138870 (14429)
Late	25C	467461 (29354)	72966 (2544)	388130 (24014)	148586 (27371)	536630 (24006)	455710 (22311)

Mean biomass of all treatment plot sizes decreases significantly post-fire for both seasons (F(9,112) = 6.66, p=0.00).

3.4.5 Resource quality

Grass height vs grass Nitrogen and grass greenness

A logistic relationship between grass height and Nitrogen content (NH4 mg/g) and total percentage greenness was done with the aim of determining if grass greenness was an accurate indicator of grass Nitrogen content.

There was a strong relationship between greenness and nitrogen content (Coef = 0.04, df = 532, p = 0.14); below about 40 % grass greenness, total Nitrogen content was always low, but swards with 100 % greenness showed a wide variation in total Nitrogen content (Figure

3.7B). Grass height was found to significantly impact grass Nitrogen content (Coef = -0.30, df = 530, p <0.00), with shorter grass (below 30 cm) having a higher Nitrogen content than taller grass (above 30 cm) (Figure 3.7C).

Using a fitted general linear model grass height and grass greenness showed that on average shorter grass was greener than tall grass (Coef = -0.02, df = 532, p <0.00), but there was a lot of scatter in the data (Figure 3.7A).

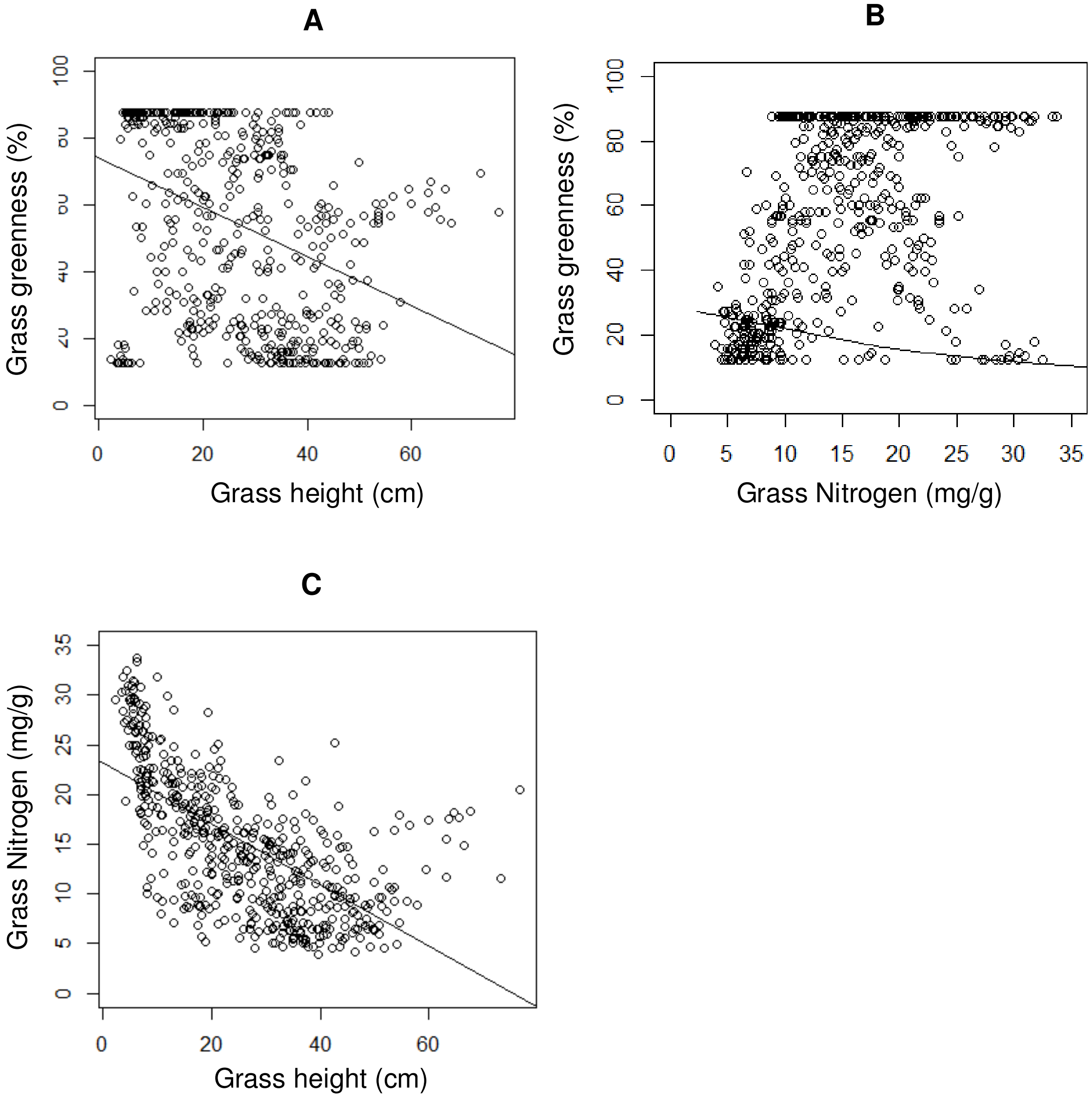


Figure 3.7 Graphs showing the significant relationship between grass height and grass greenness (A), grass Nitrogen and grass greenness (B) and grass height and grass Nitrogen (C). Lines show a logistic model fit to percentage greenness data, and a linear model fit to nitrogen data.

A multiple linear regression model was conducted comparing both grass height and grass greenness to grass Nitrogen in order to determine which factors are most important in driving nitrogen content. Both height and greenness impact nitrogen, and a model with both factors has more explanatory power than any single model (lowest AIC value - Table 3.2, Figure 3.8).

Table 3.2 Linear Model results comparing grass Nitrogen to grass height and grass greenness. The model with both factors had a much lower AIC value – indicating that it has more explanatory power.

Function	**Grass Height**		**Grass Greenness**		**AIC value**
	Coefficient	P-value	Coefficient	P-value	
Nitrogen~Height+Greenness	-0.25	0.00	0.07	0.00	3230
Nitrogen~Height	-0.30	0.00	---	---	3288
Nitrogen~Greenness	---	---	0.12	0.00	3437

The models results (Figure 3.8) demonstrates that in general short grass has a higher Nitrogen content than tall grass, and is also usually less green. However, if tall grass has a high greenness it will still have a high nitrogen content. The inclusion of ash, unburnt and burnt grass when grass was sampled could explain why some grass samples, although short and with a low greenness percentage had a high nitrogen content. Below 40 cm, grass height is a very good indicator of grass total Nitrogen content.

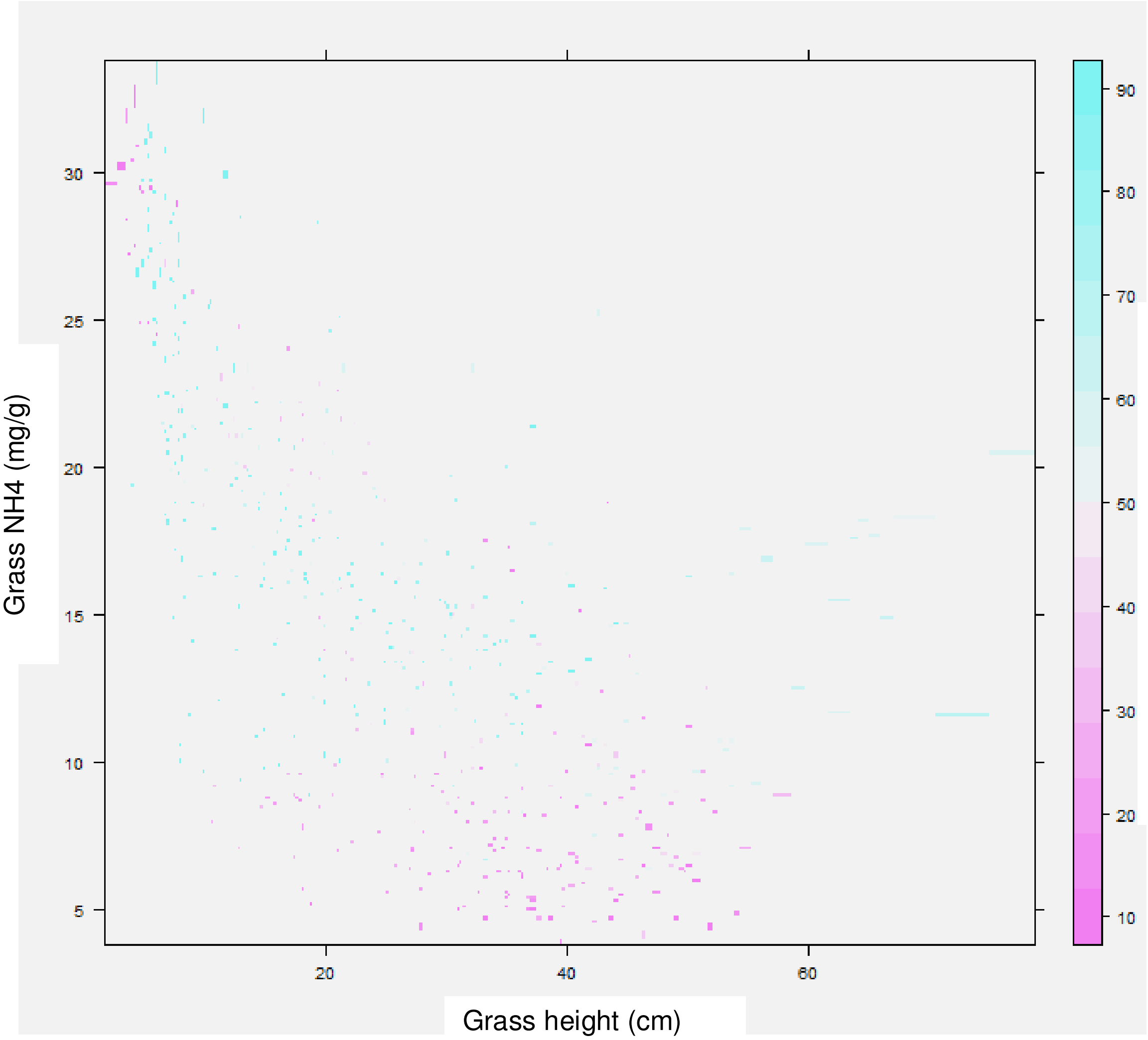


Figure 3.8 Grass Nitrogen compared to grass height and percentage greenness, with the colour coding on the right of the graph representing percentage greenness where blue is high is low greenness percentage.

Nitrogen levels over time per sampling period and season

Sampling period had a significant effect on greenness across controls (Wilks = 0.13, F(16, 492)= 56.06, p=0.00), EDS (Wilks = 0.06, F(12, 264) = 67.98, p= 0.00) and LDS (Wilks = 0.02, F(6, 266) = 259.85, p= 0.00). On the control plots grass greenness decreased between April and August (F(8, 514) = 140.45, p =0.000) after which greenness significantly increased from October until January (p=0.000) (Figure 3.9A). The pattern was similar with nitrogen (Figure 3.9B) but it took longer for nitrogen to decline than greenness during the dry season presumably because this is a sweetveld area that retains some of its nutrients in the winter.

Though interestingly, in the EDS burn plots greenness declined over time (Figure 3.9A), but %nitrogen remained high throughout the dry winter months reaching a maximum in November (Figure 3.9B). The LDS plots showed a large pulse of nitrogen after the fire (Figure 3.9B) but when the rains came this declined to values similar to the EDS burn plots. Sampling period only had a significant effect on NH4 for LDS (Wilks = 0.04, F(6, 268) = 214.58, p = 0.00).EDS greenness showed a significant decrease from April until July (p= 0.00) after which greenness significantly increased from July to November (p= 0.000) and remained stable until January (p>0.05) (Figure 3.9A). LDS greenness showed a significant decrease from August until November (p= 0.00) however there was no significant change from November till January (p=1.00) (Figure 3.9A). Interestingly EDS greenness was significantly higher post-fire than LDS and Controls (p=0.00) and remained consistently higher throughout all sampling periods (Figure 3.9A).

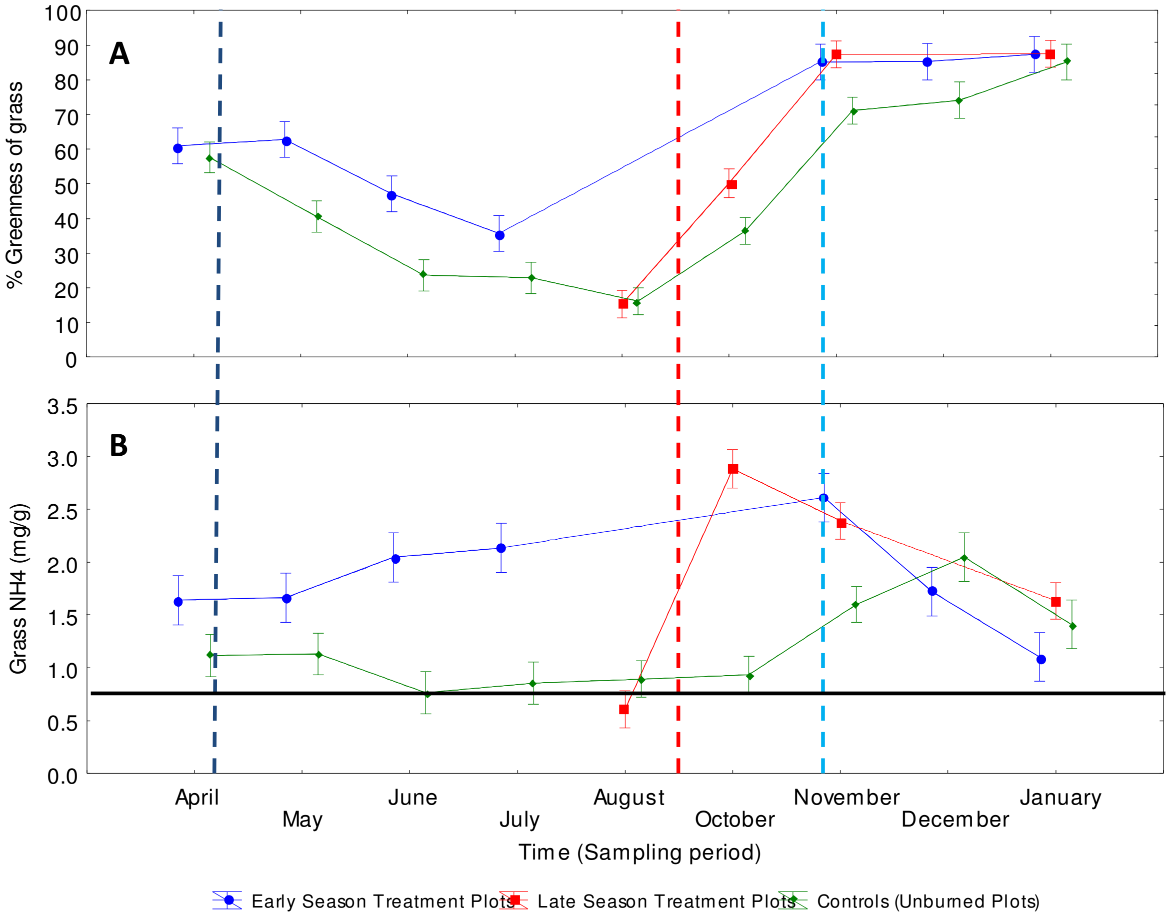


Figure 3.9 (A) Total percentage grass greenness and (B)Grass NH4 (mg/g) for EDS, LDS and controls over time. The dotted lines represent burns (EDS = dark blue; LDS = red) and start of rains (Rain = light blue). Horizontal black line indicates the maintenance value of Nitrogen for ruminants (Prins, 1996).

At the end of the study period (post-fire January), LDS had a higher NH4 than EDS (p=0.04), however was not significantly higher than the controls. By mid December sampling period NH4 content on all treatment plots had reached the same levels as the controls, which was lower than just before the onset of the rains. This is presumably because of dilution due to an increase in biomass (see Figure 3.6A), i.e the same amount of NH4 in a larger amount of biomass.

3.4.6 Distribution of environmental factors

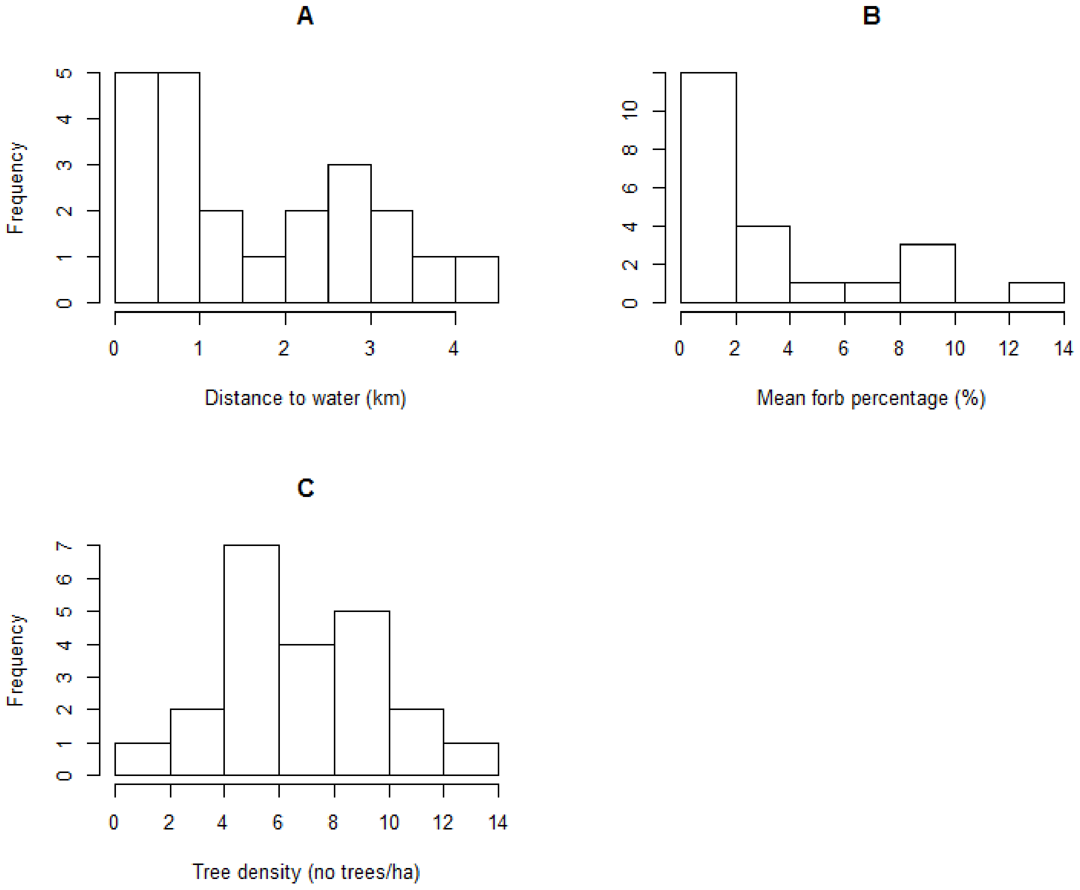


Figure 3.10 Distribution of distance to water (A), mean forb percentage (B) and tree density (C) data.

Distance to water data showed that the plots in the study site occurred between 0-5 km from water with half of the plots (10/21) occurring under 1 km to water (Figure 3.10A). Mean forb percentage data showed that the majority of the plots (16/21) had between 0-4% forbs (Figure 3.10B). Tree density data showed that an intermediate tree density of 4-10 trees/ha occurred on the majority of the plots (Figure 3.10C).

3.5 Discussion

3.5.1 Percentage transect burnt

It was predicted that EDS burns will be discontinuous and LDS burns will be continuous and this was confirmed (Figure 3.1). The EDS burns had significantly lower percentage area burnt than LDS burns and were thus more patchy on a subplot level. This is likely due to a higher percentage grass greenness and thus fuel moisture at the time of the EDS burns, as well as more benign burning conditions at the time of the fires (Figure 3.9A). Plot size had no significant influence on the total percentage area burnt (Figure 3.2). This difference in grain of burn was shown to have a significant influence on visibility in regards to reducing grass height with EDS having an average grass height 16.08 cm (std. Dev = 7.44) of compared to LDS which had an average grass height of 5.17 cm (std. Dev = 1.23) immediately post-fire (Figure 3.5).

3.5.2 Visibility and predation risk

As predicted, visibility was significantly higher on all treatment plots post-fire than on control plots and under pre-fire conditions on treatment plots. EDS burns have lower visibility than LDS burns due to differences in percentage of transect burnt between seasons (Figure 3.1) and thus a higher perceived predation risk than LDS burns (Figure 3.4A). However, if one considers the amount of time that grass remains short, the EDS fires represent a more significant impact on herbivore habitat choice than the LDS burns where the change in visibility only lasted 3 sampling intervals.

In general the effect of fire on visibility was most pronounced at 0.3 m (i.e. in the head down position). In the head down position (0.3 m and 0.5 m), a herbivore’s visibility decreased when grass height was greater than about 15 cm and 40 cm respectively (Figure 3.3A & 3.3B). In the head up position (1.0 m), a herbivore’s visibility decreased when grass height was greater than 50 cm, or remained high for all grass heights in the head up position (Figure 3.3C & 3.3D). This comparison of visibility shows that herbivores are more at risk of predation whilst grazing (in the head down position), than standing (head raised position). Lima (1987) showed, through the development of a model, that herbivores are at a higher risk of predation whilst feeding, however this risk is related to a number of factors including current predation risk as well environmental uncertainty. I can thus predict that herbivores would most likely prefer LDS plots post-fire as they have a more continuous burn rendering a higher visibility in the head down grazing position. This prediction will be tested in Chapter 4.

Fire affects grass height by removing most foliage, however it has less of an impact on shrubs where even though foliage is removed, the stem of the shrub still obstructs visibility. In areas with a higher tree or shrub density we thus expect fire to have less of an effect of increasing visibility (regardless of fire season or size) as even though foliage is removed, woody material still disrupts a herbivore's line of sight. S. Visibility decreased quickly after the onset of the rains(November), with EDS treatment plots grass height increasing to approximately 11.74 cm (std. Dev = 4.76) and LDS treatment plots 8.07 cm (std. Dev = 1.08) (Figure). Even with this increase in grass height, visibility on treatment plots for both seasons remained higher than that of controls, which had an approximate grass height of 26.26 cm (Std. Dev = 5.16)(Figure 3.5), at the end of the study period (Figure 3.4A & 3.4B).

3.5.3 Resource quantity

Even though there was no significant difference in biomass between EDS and LDS treatment plots post-fire (p>0.05), percentage transect burnt results show LDS initial post-fire biomass was lower than EDS initial post-fire biomass. After the rains, biomass increased more steeply on the LSD burns than the EDS burns (Figure 3.6), indicating that the impact of early burning and continuous grazing might have depleted stored reserves and reduced the grasses' ability to grow quickly. Biomass on treatment plots remained lower than that of controls post-fire and had not yet reached pre-fire conditions at the end of the study period. This questions if the effect of fire alone was enough to reduce biomass for the entire study period or if the impact of grazing is what has kept the grass biomass to below pre-fire conditions. Results indicate that the main impact of fire is not to increase the quantity of forage (green, uncured biomass)(Figure 3.6B), but to affect the accessibility of forage– if green shoots are interspersed with dry shoots the overall forage quality would still be lower for all but the most selective grazers. I would thus expect that non-selective grazers would respond more to fires than selective grazers (Hopcraft et al., 2010; Smit, 2011).

3.5.4 Resource quality

Based on my analysis, grass height was a strong predictor of total Nitrogen content especially for short grass, however tall grass may have a high total Nitrogen content if they have a high greenness percentage (Figure 3.8).

As predicted post-fire forage quality was higher than pre-fire forage quality for both EDS and LDS burns. When comparing greenness percentage and nutrient data analysis it was clear that although greenness percentage gave an accurate initial indication of grass nutrition immediately post-fire, it did not accurately represent the changes in total nitrogen over time on treatment plots. On controls however, grass greenness percentage was considered a good proxy for total nitrogen as both these factors follow more or less the same trend (Figure 3.9A & 3.9B).

Total N analysis results show that EDS grass quality increased gradually from post-fire June (the second month post-fire) till post-fire November after which it returned to lower nutrient conditions by January, and was thus higher than controls/the landscape for several months. This month lag (May) in grass quality increase can be attributed to a smaller total area being burnt and thus less grass being stimulated to re-grow. Thus if animals were concentrating on EDS burn plots immediately post-fire they were not utilising the plots for increased resource quality but more likely for increased visibility. The increase in total N post-fire in the LDS was immediate and much more significant than during the EDS, however it returned to landscape grass quality within a much shorter time (three months). This may be attributed to more total area being burnt and thus less grass re-growth occurred and nutrients were concentrated in the low amount of biomass (Figure 3.6B). Total N for both EDS and LDS decreased after the onset of the rains in November. This is probably due to an increase in grass growth and thus the dilution of nutrients among a larger amount of biomass (Figure 3.6B)

These results suggest that initial LDS post-fire resource quality is higher than EDS. Fire thus affects the accessibility (proportion of a grass sward consisting of new, more nutritious re-growth) of the green biomass and not necessarily the quantity available.

3.5.5 Environmental factors

Environmental factors have been briefly analysed (Figure 3.10). The results generated in this chapter will be combined with that of dung data in chapter four in order to determine if they in fact have had a significant impact on the attraction of herbivores.

3.6 Conclusion

Fire has been shown to influence both resource quantity, quality and landscape of fear in different ways depending on fire season. Fire size had a minimal effect on resource quality. This can be due to fire having the same effect on the area regardless of plot size as it is an “unselective consumer” as fuel properties at the time of the burns were similar on all plot sizes.

In summary, EDS burns are discontinuous, have a lower visibility (at ground level) and thus higher perceived predation risk. They re-grow biomass more slowly after rains than LDS burns which, in contrast, are continuous, have a higher visibility and thus lower perceived predation risk. Forage on the LDS burns is also greener with higher N content than the EDS burns, but this lasts only a short time whereas the increased N content on the EDS burns persists throughout the dry season. Results show that when grass height is lower than 20 cm it has a higher nutrient content than grass taller than 20 cm (Figure 3.7A), lower than 40 cm it has a higher percentage greenness than grass taller than 40 cm (Figure 3.7B). Grass height, which is initially affected by fire, thus plays an important role in determining the accessibility of forage in regards to how much of the grass sward is burnt and thus how much re-growth is stimulated. Below 40 cm, grass height is a very good predictor of total Nitrogen content.

Control plots had very similar amounts of green biomass compared with burned plots at all time steps (Figure 3.6B), the differences are therefore in the availability of this green biomass and the ease with which herbivores can access high-quality forage.

Obviously the effect of the fires lasted longer on the EDS burn plots than the LDS plots because grass productivity was stimulated by rainfall. Whether active grazing on the EDS plots contributed to keeping the grass sward short, with high nitrogen content and high visibility, is not yet clear, but the fact that biomass grew back more slowly on the EDS plots suggests that this early burn treatment did affect grass productivity. This chapter has looked at the influence of fire on the landscape, so as to set the scene for understanding how herbivore habitat preferences and behaviour are altered by fires of different seasons and sizes.

4 CHAPTER 4: WHY DO HERBIVORES USE BURNT AREAS? UNRAVELLINGTHE RELATIVE IMPORTANCE OF RESOURCE QUALITY AND QUANTITY AND REDUCED PREDATION RISK

4.1 Introduction

Fire and herbivory both consume above ground biomass, however there are distinct differences between these two disturbances with fire being unselective and consuming all materials whereas herbivory is selective in consuming only edible material (Bond & Keeley, 2005). Disturbances such as fire and grazing act as ecosystem engineers and influence primary production which in turn determines the spatial and temporal distribution of both predators and prey as well as utilization of the landscape based on the balance between food and safety (Hunter & Price, 1992; Naiman et al., 2003; Anderson et al., 2010; Hopcraft, Olff & Sinclair, 2010).

Fire affects plant and soil nutrient cycling (Bond, 2005), modifies plant diversity and plant species composition as well as causes changes in tree cover and vegetation structure (Eby et al., 2014). Fire impacts vegetation by removing moribund material (Bond, 2005) which is replaced by re-growth, also referred to as a green-flush (McNaughton, 1983; Allred et al., 2011). Herbivores have been shown to be attracted to this post-fire vegetation (Van de Vijever et al., 1999; Moe & Wegge, 1997; Archibald, 2008; McNaughton, 1983; Klop et al., 2007). Whether this is driven by herbivore attraction to a good forage resource (bottom up), or attraction to a landscape which reduces fear of predators (top down) is poorly understood (Riginos & Grace, 2008; Burkepile et al., 2013).

The relative importance of top-down vs. bottom up forces varies from one biological system to another and within one system due to heterogeneity (Hunter & Price, 1992; Herendeen, 2004). Environmental heterogeneity, including season, are important in determining the strength, relative importance and interactions of these factors (Hunter & Price, 1992: Anderson et al., 2010).

Resource quality and quantity as bottom-up drivers of herbivore distribution

In order to understand the selection of forage resources by ungulates it is important to understand each species' forage needs as this forms the underlying basis of competitive interactions. Hanley (1982) describes four factors which determine food partitioning - body size, digestive systems, rumino-reticular volume and mouth size. Body size influences an animal's basal metabolic rate and thus determines the animal's energy requirements and thus the amount and quality of food that is required. Smaller animals have higher metabolic rates than larger animals and focus on quality and not quantity of plant material intake (Demment & Van Soest, 1985; Owen-Smith, 2002).The type of digestive system interacts with body size in determining the quality and quantity of food intake (Hanley, 1982). Body size and subsequent herbivore body weight determines the food requirements of that herbivore due to costs of maintenance. Large-bodied herbivores require more nutrients per day than small-bodied herbivores, however they cannot afford the time to be selective where as small-bodied herbivores can (Hanley, 1982). Herbivores are divided into two groups based on their digestive system, namely ruminants (foregut fermenters) and non-ruminants (hind-gut fermenters) (Hairston et al., 1960; Hanley, 1982). Ruminants or foregut fermenters have four chambered stomach and digestion occurs before absorption. Non-ruminants or hind-gut fermenters have a single stomach and digestion occurs after food has passed through the stomach (Hanley, 1982). Gut capacity (rumino-reticulum volume) and metabolic rate work hand in hand with body size to determine rate of ingestion. As body size increases, metabolic rate decreases and gut capacity increases, hence large-bodied herbivores have a slower rate of digestion than small-bodied herbivores which have a high metabolic rate and low gut capacity (Demment & Van Soest, 1985). Ruminants focus more on forage quality than quantity and non-ruminants focus more on forage quality than quantity due to rate of ingestation. Mouth size determines how selective a herbivore can be, this in turn influences whether a herbivore is forage quality or quantity driven: the smaller a herbivore's mouth, the more selective it can feed and thus the more forage quality driven that herbivore is (Hanley, 1982). Hairston et al. (1960) suggested that resource availability is the primary regulator of herbivore populations and that inter-specific competition for resources outweighs the impact of predation (Hairston et al., 1960).

Predation as a top-down driver of herbivore distribution

The study of anti-predatory behaviour of prey and hunting behaviour of predators forms the basis of predator-prey interactions. Brown (2010) stated that the ecology of fear drives the ecology of predator-prey interactions and influences all aspects of this interaction in regards to population and evolutionary dynamics, the coexistence of species and the spatial and temporal use of the landscape (Brown, 2010; Laundre et al., 2001).

Predators can affect prey consumptively or non-consumptively (Matassa & Trussell, 2011). Consumptive effects of predators refers to the direct removal of prey thus reducing prey density and in turn reducing consumer pressure on plant resources (Matassa & Trussell, 2011; Brown, 2010; Cooper, 2008). Non-consumptive effects of predators refers to the "scaring of prey" through the creation of a landscape of fear where animals respond to predation risk by decreasing foraging rates (Brown, 2010; Matassa & Trussell, 2011;

Laundreet al., 2001). Brown (2010) and Matassa & Trussell (2011) both argue that the non-consumptive effects of predators are as or even more important than the consumptive effects. Predation risk impacts prey behaviour and resource use in regards to where, when and what prey species consume, this in turn impacts prey use of the landscape (Matassa & Trusssell, 2011; Laundre et al., 2001). This fear response of prey to predation is important in maintaining coexistence and promotes biodiversity.

Prey response to predation risk varies from species to species, from habitat to habitat (Laundre et al., 2001; Cooper, 2008; Cooper & Frederick, 2007; Blumstein et al., 2003) and over time diurnally and seasonally (Brown, 2010). Prey response includes behavioural changes in foraging strategies, vigilance (Laundre et al., 2001; Kramer & Bonenfant, 1997) and escape behaviour (Cooper, 2008). The reaction of prey species to predation risk is referred to as escape behaviour (Brown, 2010; Laundre et al, 2001; Cooper, 2008; Cooper & Frederick, 2007). There are various escape behaviour strategies, these include the avoidance of high risk areas, fleeing and monitoring (Kramer & Bonenfant, 1997). Animals have however been found to use areas with high predation risk. This usually occurs when there benefit from the resource in that area outweighs the risk (Brown, 2010).

Cooper (2008) makes a key distinction between two prey behavioural responses to predation risk, namely monitoring and vigilance. Monitoring occurs when a predator has been detected and the prey is under actual predation risk. Vigilance occurs before a predator has been detected and the prey is under perceived predation risk (Cooper, 2008).

If a prey species reacts behaviourally to the presence of predators by reducing or increasing an activity or use of an area, it can indirectly affect a resource. However Werner and Peacor (2003) also point out that a change in resources can alter herbivore behaviour as well. Fire, and its impact on vegetation structure and hence visibility, affects the vigilance behaviour of animals (Eby et al., 2014). Vigilance can affect the rate of energy flow by reducing the amount of time available for the animal to forage (Fortin et al., 2004). The portion of time spent on individual vigilance decreases as group size increases.

Satara and surrounding areas in Kruger National Park are known for resident lion (*Panthera leo*) populations and much research has been conducted on population dynamics and variables influencing these populations (prey availability, disease etc.) in Kruger National Park (Funston et al., 1998; Funston et al., 2001; Ferreira & Funston, 2010; Smuts, 1976). Lions prey species preference is influenced by a variety of factors including prey species abundance, body size, anti-predatory behaviour, herd size and habitat use (Funston et al., 2001; Hayward & Kerley, 2005). Vegetation structure, influenced by management practices, fire and elephants (*Loxodonta africana*), has been suggested to influence predator ambush opportunities and subsequently herbivore foraging behaviour (Loarie et al., 2013). During an analysis of various studies, Hayward and Kerley (2005) showed that zebra were recorded in 40 studies, blue wildebeest in 38 studies and impala in 34 studies as lion prey. They further deduced that zebra and blue wildebeest were considered preferred prey species and impala an avoided prey species. These results were based on various factors including each species injury threat, body size, species abundance and anti-predatory response (Hayward & Kerley, 2005).

Environmental factors that influence spacing of social animals based on predator avoidance, include vegetation structure (which determines visibility range), and landscape features, such as distance to water (increased vigilance closer to water) (Beecham & Farnsworth, 1999, Valeix et al., 2009; Crosmary et al., 2012).

Body size

Body size is suggested to be responsible for the variation in importance of resource versus predation (Hairston et al., 1960; Eby et al., 2014). Variation in grazer body size promotes coexistence due to each body size being related to a preference for a certain forage quality (Sensenig et al., 2010). As mentioned above body size and digestive system determine resource partitioning in regards to forage quality and quantity (Sensenig et al., 2010; Smit, 2011; Klop et al., 2007).

Sensing et al, (2010) state that bottom-up forces such as quality and quantity of resource are not sufficient to explain herbivore habitat preference and that selective predation pressure plays an important role in distributing herbivores. Thus body size can be described as a function of both bottom-up and top-down forces (Sensenig, Demment & Laca, 2010) – with smaller bodied animals being more susceptible to predation (although this also depends on social characteristics)

Smaller-bodied herbivores (< 300 kg) have a restricted range of forage quality, whereas larger-bodied herbivores (> 300 kg) can use a much wider range (Smit, 2011). Small herbivores are influenced by both forage quality as well vegetation-mediated predation risk (Sinclair et al., 2003). This is due to smaller herbivores having a higher metabolic rate so they need high quality forage to maintain their metabolism (Smit, 2011) and less visibility in tall vegetation based on their body size (Eby et al., 2014). Large herbivores are influenced mainly by forage quantity and not predation risk (Burns et al., unknown; Sinclair et al., 2003). This is due to larger herbivores having a slower metabolic rate (Smit, 2011) and higher visibility in tall vegetation (Hopcraft et al., 2011; Eby et al., 2014; Sensenig et al., 2010). Hopcraft et al. (2010) and Scholes et al. (2003) both suggest that for medium-sized herbivores (such as zebra and wildebeest), bottom-up forces in the form of nutrition is the most important regulatory factor.

This study focused on three herbivore species, representing three body sizes, namely impala (small-bodied ruminant herbivore), blue wildebeest (medium-bodied ruminant herbivore) and Burchell's zebra (medium-large bodied non-ruminant herbivore) (Table 4.1). We hypothesised that the response to landscape of fear and resource use varies between these species due to difference in body size, and that comparing between fires of different sizes (which differ in terms of resource quantity and visibility – Chapter 3) and seasons (which differ in terms of visibility – Chapter 3) we might be able to determine what was driving the use of burned areas for different herbivore types. These three species were selected due to high population numbers occurring in the study site (Gertenbach, 1983).

Impala (Aepyceros melampus)

Impala occur in herds of 6-20 animals or congregations consisting of 50-100 animals under favourable environmental conditions. Their social structure consists of males which are only territorial during the rut which occurs during autumn, bachelor herds consisting of adult and juvenile males and breeding herds consisting of adult and juvenile males and females (Skinner & Chimimba, 2005). Temporary nursery herds also occur and consist of juveniles which later re-join the breeding herd. Bachelor herds occupy areas away from the breeding herds and thus avoid competition for resources (Murray, 1980). Calving season takes place between November and January (Fairall, 1972).

Impala vigilance increases with increasing predator density (Hunter & Skinner, 1998). They only flee once a predation threat has entered their flight distance, when the threat is beyond this distance they observe. Impala have also been described to practice "mobbing" as an anti-predatory behaviour (Hayward & Kerley, 2005). When fleeing impala leap over shrubs and disperse in all directions after which they regroup (Skinner & Chimimba, 2005). When startled, impala are observed to kick-back, particularly in thick bush (Kingdon, 1982). The injury threat level of impala to lion is recorded as 0 on a scale of 0-2 (Hayward & Kerley, 2005). Impala are diurnal with very little activity at night. Impala require both cover and water in their habitat (Rowe-Rowe, 1994). Shrubs and trees provide cover from the elements and offer forage resources. They are water dependant and usually remain within 8km of water (Young, 1972).

Impala are mixed feeders, using both browse and graze resources in different ratios depending on availability and season (Hofmann, 1973). Browse is an important resource during winter months when most grasses begin to cure. Forbs are also found in their diet

(Skinner & Chimimba, 2005). It has been argued that due to the fact the impalas are mixed feeders and not obligate grazers, their use of burnt areas cannot be compared to that of wildebeest and zebra. Our data can test this, we aim to determine whether impala use burnt areas for grass or browse resources through behavioural observations (Figure 4.9).

Blue Wildebeest (Connochaetes taurinus)

Blue wildebeest usually occur in herds of 20 to 30 individuals. Their social structure consists of territorial males, female herds and bachelor herds. Territorial males in Kruger National Park have been found to maintain their territories throughout the year instead of the more common seasonal maintenance of a territory (Fairall, 1968). During the rut, which in Kruger National Park is between April and June, the majority of blue wildebeest bulls remain in bachelor herds or solitary (Braack, 1973). Bachelor herds consist of adult and young males which do not have territories. Bachelor herds are found in areas on the fringes of the breeding or nursery wildebeest population and thus do not compete for resources (Skinner & Chimimba, 2005). Calving season takes place from November and can last up to May depending on favourability of environmental conditions (Fairall, 1968).

It has been found that blue wildebeest vigilance increases with increasing predator density (Hunter & Skinner, 1998) and practice a “flee” anti-predatory defence (Hayward & Kerley, 2005).They are rated as having an injury threat level to lions of 0 on a scale of 0-2 (Hayward & Kerley, 2005). Blue wildebeest have been observed spending approximately 50 % of their time standing/resting or lying down. They are able to meet their nutritional requirements through short feeding sessions and actively graze at night; however they are significantly less active at night than during the day (Skinner & Chimimba, 2005). Blue wildebeest are known to “follow the rains” and are sensitive to localised rainstorms where they move towards the rain in search of grazing (Talbot & Talbot, 1963). Wildebeest are water dependant and drink mainly in the morning (Skinner & Chimimba, 2005).

Blue wildebeest are grazers which have a preference for short grass heights and rarely graze grass which is more than 100-150 mm high. Thus grazing lawns and green-flushes on burnt areas are expected to be particularly attractive. Their wide snout allows for effective cropping of short grass but is less effective on tall grass where leaves have to be selected and stripped. Blue wildebeest show a seasonal preference to different grass species (Skinner & Chimimba, 2005). Whyte (1985) states that in Kruger National Park blue wildebeest populations could be limited by lion predation during years when high rainfall has allowed short grass areas to grow. A decrease in visibility has been suggested as a cause for this increased predation (Whyte, 1985).

Burchell's Zebra (*Equus quagga*)

Zebra occur in small family groups consisting of a stallion and 1-5 mares with their foals. Zebra herds consist of many family groups. Foals are born throughout the year, however in Kruger National Park they tend to foal between October and March with a peak occurring between December and January where over 85% of foals are born (Smuts, 1976). Smuts (1974) states that precipitation and the subsequent green growth are large factors contributing to this peak.

Zebra practice "active defence" as an anti-predatory response and are known to chase and even injure or kill predators. Subsequently their injury threat level to lions is recorded as a 2 on a scale of 0-2 (Hayward & Kerley, 2005). They are considered a savanna species and prefer open woodland, shrub and grassland areas. They are water dependant, moving between 10 and 12 km from a water source (Smuts, 1972). Zebras leave summer grazing areas before the water resource is depleted (Smuts, 1972)

Zebras are bulk grazers and graze a wide variety of grass species (Skinner & Chimimba, 2005). Zebra usually feed on long grass but are however partial to burnt areas and will graze on both new re-growth as well as scorched grass (Smuts, 1972). Smuts (1974) suggests that the dense vegetation in Kruger National Park, which increases predation risk and loss of contact with the herd, inhibits larger group sizes. Stallions take up the rear of the group when moving and are more prone to predation (Skinner & Chimimba, 2005).

Table 4.1: Summary of impala, blue wildebeest and zebra characteristics (Hayward & Kerley, 2005; Kleynhans, E.J. et al*.,* 2010).

Characteristic	**Impala**	**Blue Wildebeest**	**Burchell's Zebra**
Body Weight (kg)	40-63	163-252	220-320
Digestive System	Ruminant	Ruminant	Non-ruminant
Body size (s/m/l)	Small-bodied	Medium-bodied	Medium-large bodied
Feeding style	Mixed/intermediate feeder	Selective grazer	Bulk grazer
Forage quality vs. quantity	Quality	Quality	Quantity
Preferred grass height (mm)	< 400 (short-tall)	100-150 (short)	>400 (short-tall)
Feeding time	Day (Minimal at night)	Day and Night (less at night)	Day and Night (less at night)
Injury threat level to lions (0-2)	0	0	2
Preference to lions	Avoided prey species	Preferred prey species	Preferred prey species
Anti-predatory behaviour	Mobbing	Flee	Active defence

4.2 Aims and Objectives

This study aims to determine the relative importance of resource quality and quantity and predation risk in determining herbivore use of burned areas. I did this by monitoring herbivore presence and behaviour on burn scars of various sizes that burned in different seasons (different patchiness). The previous chapter (Chapter 3) described the impact of fire on the physical environment, this chapter focuses on herbivore response to these changes in the physical environment.

The following hypotheses, associated with two main research questions, will be tested:

1. How does fire size influence the relative importance of resource quality and quantity and predation risk?
   - I predict that if resource quality is the dominant driving factor of herbivore use of burnt areas then there will be no significant difference in herbivore occurrence across all burn sizes because resource quality does not differ among plots (Chapter 3), however herbivore presence will be lowest on control plots. Zebra, wildebeest and impala will show no preference for burn size.
   - I predict that if resource quantity is the dominant driving factor of herbivore use of burnt areas, then medium-bodied herbivore/bulk grazer presence (zebra) will be higher on larger burn areas and small-bodied herbivores/selective feeders (impala and wildebeest) will occur on all burn sizes.
   - I predict that if predation risk is the dominant driving factor of herbivore use of burnt areas then herbivore presence will be lowest on control plots and will increase with fire size, with the largest fire size having the highest herbivore presence. Wildebeest and zebra, which are the preferred prey species of lions in the study area would be expected to show a preference for the largest fire size.
2. How does fire season influence herbivore presence and behaviour on burnt areas?
   - I predict that herbivores on EDS burns will have higher vigilance behaviour than herbivores on LDS burns. This is due to higher visibility on LDS burns than EDS burns as a result of differences in percentage of transect burnt between seasons (Chapter 3; Figure 3.1).
3. Environmental factors such as distance to water, tree density and forb percentage could possibly override or help explain results obtained. Based on literature discussed in Chapter 3, I predict that:

- Plots closer to water will be used more than burn plots further from water.
- Plots with higher percentage forbs will be used more than burn plots with lower percentage forbs.
- Plots with higher tree density will be used less than burn plots with lower tree density.

4.3 Data Analysis

To determine which data collection method represented animal presence most accurately, a comparison of dung and camera trap pictures and total number of animals per hectare from observations was conducted. Total number of animals per hectare was calculated by determining the proportion of each plot in the study site visible during animal observations. This proportion was multiplied with the total number of animals of all three species viewed on each plot to determine the total number of animals per hectare per sampling period.

Ideally one would analyse these data using a mixed effects model, where the response of data for each subplot was assessed with burn plot as a fixed effect (and other environmental variables such as distance to water, forb cover etc could be added as random effects). However, I chose to use a more directed approach where I looked at particular relationships between my response and driver variables.

Dung count data for all three herbivore species (impala, blue wildebeest and zebra) was averaged across subplots and plots to make it comparable across fire size. A Repeated Measures Analysis of Variance (ANOVA) was used to determine whether the frequency of dung per plot (proxy for animal use per plot) varied with season over the sampling periods. Mean dung count data was analysed per sampling period (regardless of plot size), per plot size (regardless of sampling period) and per sampling period per plot size respectively. A univariate Analysis of Variance (ANOVA) was used to determine changes in dung count data with plot size and season.

The mean number of camera pictures per day and night, per day and per night was calculated for impala, wildebeest and zebra for each sampling period. A Repeated Measures Analysis of Variance (ANOVA) was used to determine whether there was a difference in animal numbers over time, among seasons and with plot size. A univariate Analysis of Variance (ANOVA) was used to determine changes in camera pictures with plot size and season.

The proportion of behavioural activities was recorded by dividing the number of animals performing a specific behaviour by the total number of animals observed per scan (behavioural activities did not differ between scans and therefore the data from both scans were averaged per plot per replica per species). Proportion vigilant was used as a proxy of perceived predation risk, with the higher proportion vigilant the higher the perceived risk of predation by an animal. Proportion grazing was used as a proxy of use of grass resource. Proportion resting/lying down was also used as a proxy of perceived predation risk, with animals spending a high proportion of time grooming or resting/lying down when there is a low perceived predation risk. Due to a lack of EDS pre-fire observation data, comparisons of animal behavioural data have been made between pre-fire to post-fire data regardless of season using an univariate Analysis of Variance (ANOVA).

A chi-square analysis was used to determine differences between impala proportion grazing and browsing. This was done to determine if grass resource quality and not browse was attracting impala. This test also serves to motivate the comparison of a mixed feeder to grazers.

A Students T-test for independent sampling groups was conducted to compare mean dung counts of all three species across mean grass heights of less and more than 20 cm. The aim of this analysis was to determine if herbivore species showed a preference for certain grass height categories (Table 4.1) as literature suggests. The same statistical analysis was performed to compare proportion of time spent vigilant and grazing to mean visibility in when grazing (in the head down position) (Table 4.4).

Tree density, forb percentage (under pre-fire conditions) and distance to water were compared to mean pre-fire dung counts for all three herbivore species (impala, blue wildebeest and Burchell’s zebra) using a Pearson’s correlation. All three environmental factors were divided into low or high categories (lower or higher than the average of that factor) and a T-test was conducted to determine if there was any significant difference in mean dung on the study plots Figure 3.10 (Chapter 3) represents the variation in tree density, forb percentage and distance to water data in the form of histograms.

4.4 Results

4.4.1 Dung counts

Dung counts for all three species were summed across all sampling periods and seasons as were camera trap pictures (day and night). The summed data (dung count and camera trap) were then used to determine if there was a correlation (r = 0.257) between these two measures of animal presence (Figure 4.1A). The sum of all three species dung and total number of animals per hectare were used to determine if there was a correlation (r = 0.068) between these two measures of animal presence (Figure 4.1B). Dung count data was the best measure of animal presence (Figure 4.1A and 4.1B) as there were many occurrences where dung was present however no pictures had been recorded or animals observed.

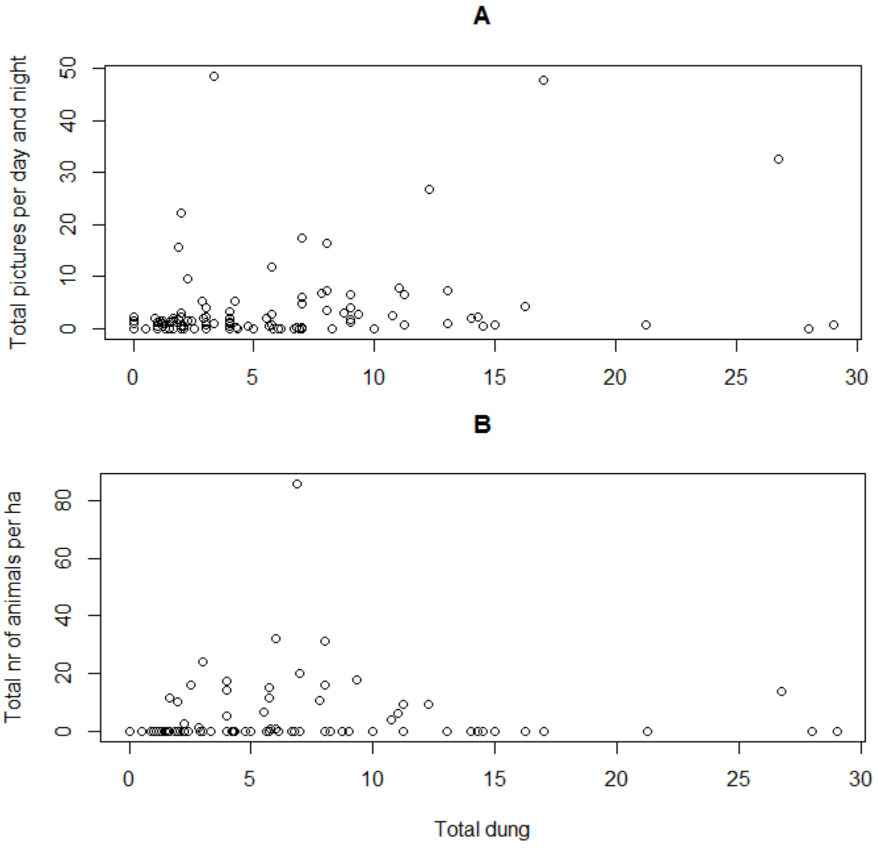


Figure 4.1 (A) Correlation of total number of camera trap pictures per day and night and total dung count for all three herbivore species throughout the study period. (B) Correlation of total number of animals per hectare and total dung count for all three herbivore species throughout the study period.

Fire season

Time/sampling period did have a significant impact on mean dung counts in the EDS (Wilks = 0.30, F(12,87.60) = 4.19, p = 0.00), but was not significant for LDS (Wilks = 0.71, F(9,73.16) = 1.23, p = 0.29) and control plots (Wilks = 0.33, F(24, 61.51) = 1.21, p = 0.27).

Under pre-fire conditions mean dung counts for all three species did not differ between EDS, LDS treatments and control plots (t = -1.08, df = 103.74, p = 0.28). Impala EDS mean dung increased immediately post fire (May p = 0.80, June p =0.49) but this increase was only significant from July (p=0.03) to December (p=0.04). Dung counts stabilised from July to December (p=0.99). Impala LDS mean dung increased from October to November after which it stabilised till January. These changes in LDS were not significant (p>0.05) (Figure 4.2A).

Blue wildebeest EDS mean dung did not increase significantly post-fire until December. December dung count was significantly higher than all the previous sampling periods (pre and post-fire) (p<0.05). There were no significant changes in LDS dung counts however trends in the data show that dung increased post-fire and remained relatively constant from November to January (Figure 4.2B). Zebra EDS mean dung did increase immediately post-fire however this increase was short lived and not statistically significant (p= 0.08). Trends in the data show that zebra mean dung decreased from May to July and increased again till December, however these increases were not significant. Zebra LDS mean dung did not increase post-fire and remained stable throughout LDS sampling (p>0.05). There were slight fluctuations in the mean dung counts of all three species on the control plots over sampling periods, however these changes were not statistically significant (p>0.05).

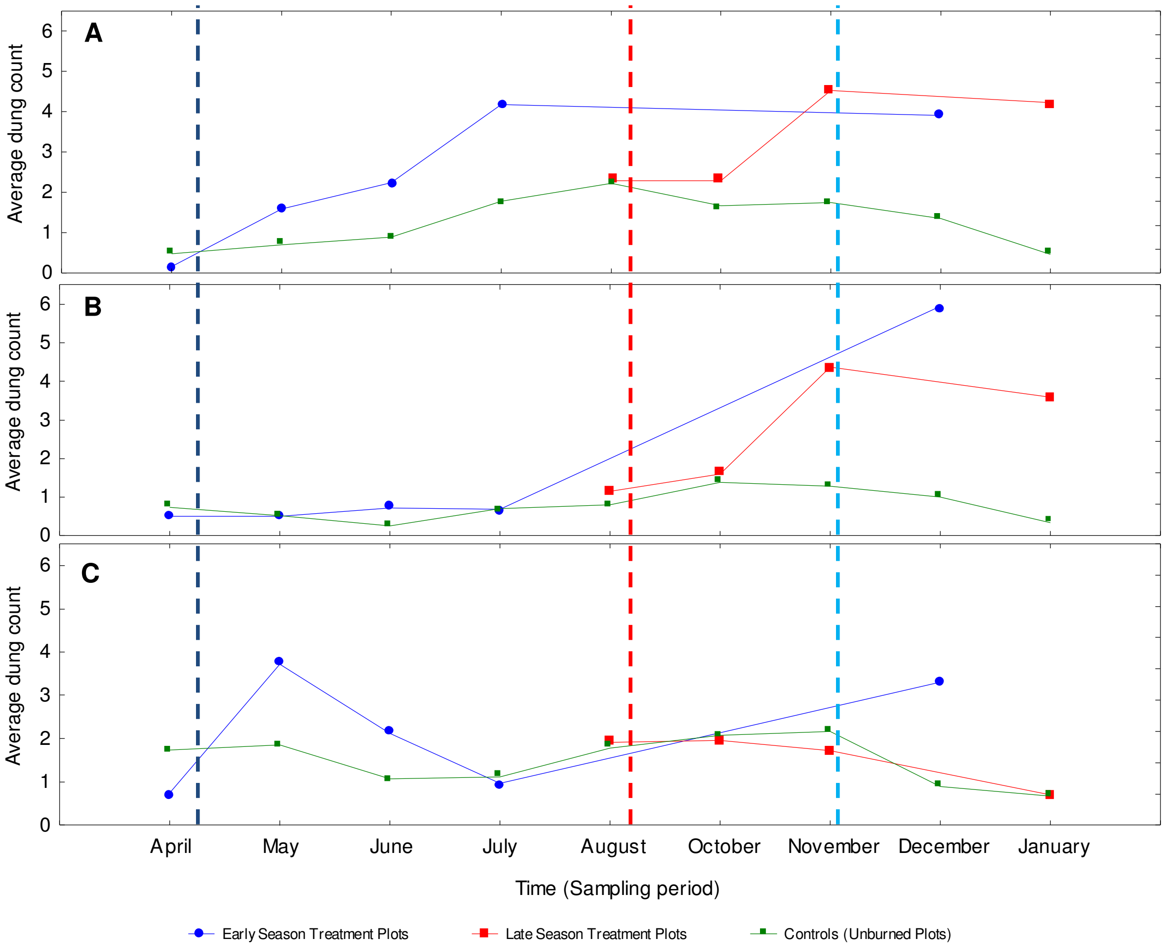


Figure 4.2 Mean dung count per sampling period regardless of fire size for impala (A), wildebeest (B) and zebra (C) over time (sampling period) for EDS, LDS and controls, regardless of plot size. The dotted lines represent burns (EDS = dark blue; LDS = red) and start of rains (Rain = light blue).

Fire size

There was no significant difference in mean dung count under pre-fire conditions for all three species across plot sizes for both EDS and LDS (p>0.05). For EDS post-fire sampling, only zebra mean dung count showed a significant difference with 5 ha treatment plots containing significantly more dung than control plots (F(2,42) = 4.15, p = 0.02) (Figure 4.3A). For LDS post-fire sampling, only wildebeest mean dung count showed a significant difference with 5 ha treatment plots containing significantly more dung than control plots (F(3,35) = 3.15, p=0.04) (Figure 4.3B). In the EDS, the 5 ha treatments plots had significantly more dung for all three species than on control plots (F(2,53) = 3.63, p=0.03). There was no significant difference in mean dung counts for all three species across plot size for LDS (F(3,48) =3.07, p>0.05).

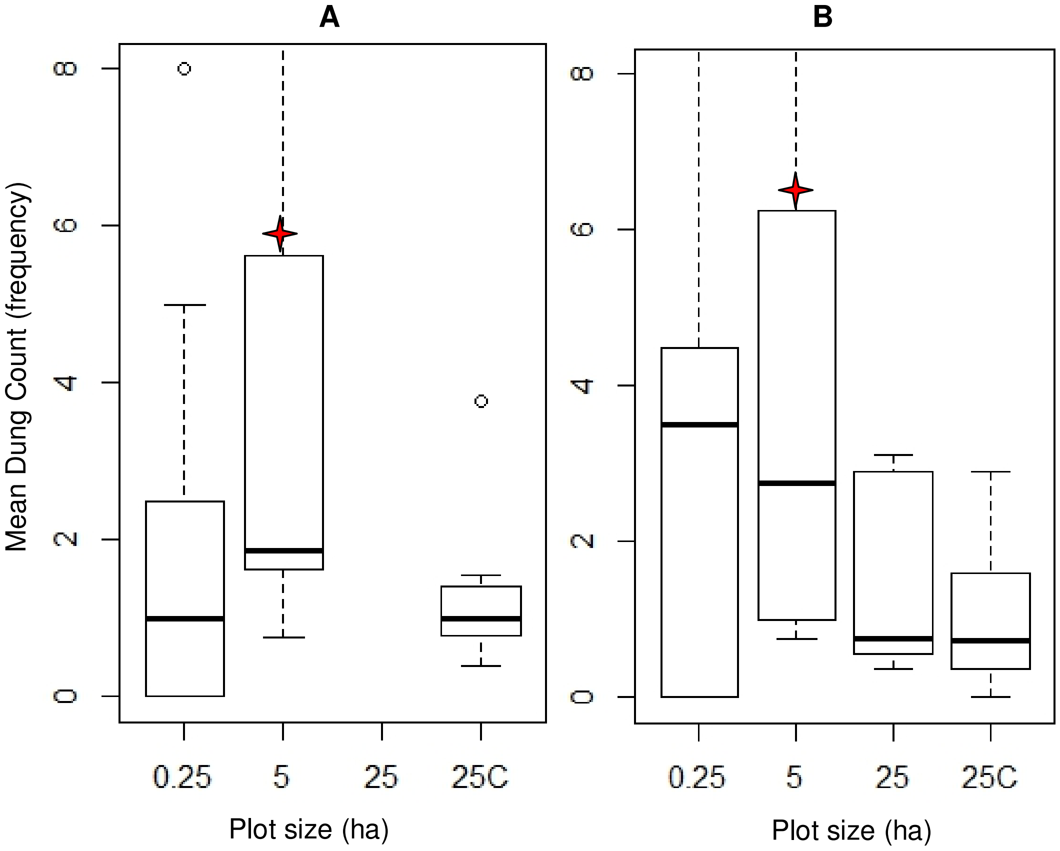


Figure 4.3 Mean dung count per fire size regardless of fire season for (A) Zebra during EDS post-fire and (B) Wildebeest during LDS post-fire across plot size. Star symbols represent the plot size with statistically higher mean dung counts than controls (25C).

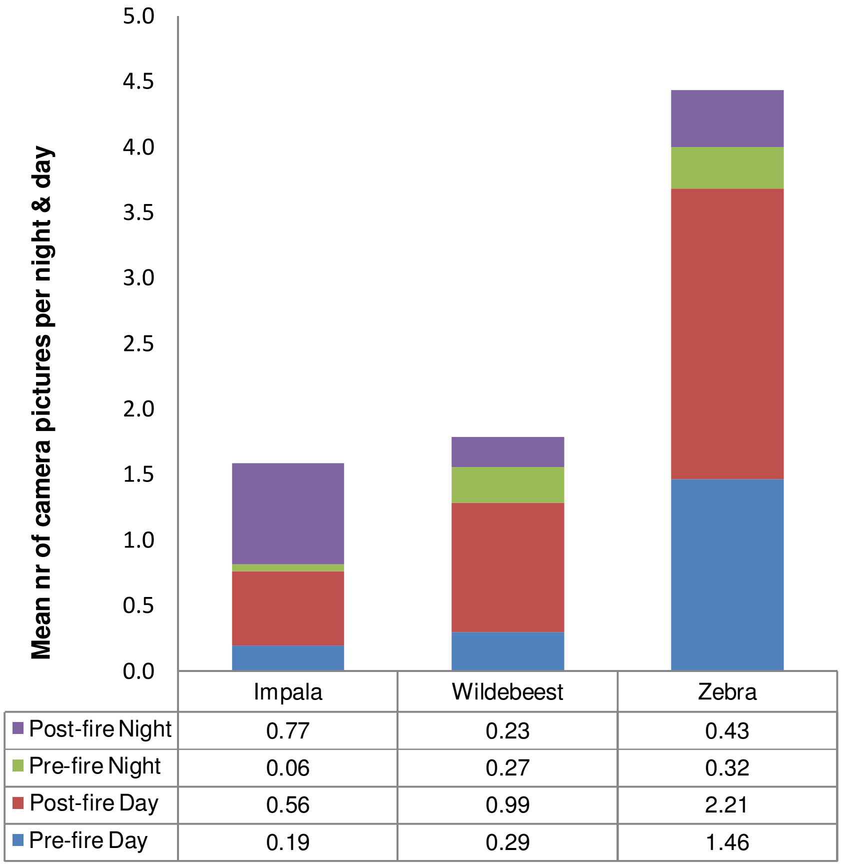
On controls, for all species, there is no significant difference in mean dung counts over sampling periods. Thus controls were used consistently throughout EDS and LDS sampling (Table 4.2). Over the EDS and LDS sampling periods there was no significant difference in mean dung counts on 0.25ha treatment plots. For wildebeest there was significantly higher mean dung count (F(8,23) = 7.831) during post-fire December (p= 0.00) sampling on 5ha treatment plots for EDS and post-fire November sampling for LDS (p=0.01). In regards to 25ha LDS treatment plots wildebeest dung was significantly more frequently encountered post-fire than pre-fire August sampling (F(3, 116) = 31.15, p = 0.00).

Table 4.2 Table showing the mean dung count per species per fire size and standard deviation in brackets under pre-fire conditions (EDS = April 2014, LDS = August 2014), immediately post-fire (EDS = May 2014, LDS = October 2014) and during the last sampling period for both EDS and LDS (January 2015). Bold figures represent occasions where a significant result was obtained in the above analysis.

Season	Species	Plot	Pre-fire	Immediately post-fire	Last sampling
EDS	Impala	0.25	0 (0)	1.25 (1.89)	3.25 (5.25)
	Impala	5	0.31 (0.47)	1.94 (1.25)	4.56 (1.61)
	Impala	25C	0.48 (0.17)	0.70 (0.51)	1.35 (0.96)
	Wildebeest	0.25	0.75 (0.96)	0.50 (0.58)	4.50 (8.35)
	Wildebeest	5	0.25 (0.20)	0.50 (0.84)	7.38 (1.36)
	Wildebeest	25C	0.74 (0.34)	0.52 (0.63)	1.00 (0.85)
	Zebra	0.25	0.75 (0.50)	3.25 (3.40)	2.00 (2.16)
	Zebra	5	0.75 (0.89)	4.19 (3.34)	**4.63 (3.35)**
	Zebra	25C	1.74 (0.78)	1.85 (1.68)	0.90 (0.42)
LDS	Impala	0.25	3.5 (3.11)	3.75 (1.71)	5.25 (8.54)
	Impala	5	1.08 (0.38)	1.58 (1.88)	5.17 (3.11)
	Impala	25	1.67 (2.04)	0.44 (0.16)	0.8 (0.03)
	Impala	25C	2.22 (2.25)	1.67 (1.46)	0.46 (0.34)
	Wildebeest	0.25	2.00 (2.16)	2.25 (2.22)	**4.25 (5.32)**
	Wildebeest	5	0.50 (0.50)	1.42 (1.15)	**4.67 (3.19)**
	Wildebeest	25	0.45 (0.47)	0.60 (0.06)	0.63 (0.38)
	Wildebeest	25C	0.81 (1.05)	1.39 (0.98)	0.35 (0.33)
	Zebra	0.25	1.75 (1.50)	1.00 (2.00)	0.25 (0.50)
	Zebra	5	2.50 (0.87)	3.17 (4.63)	1.5 (0.00)
	Zebra	25	1.39 (0.71)	2.04 (0.57)	0.39 (0.09)
	Zebra	25C	1.78 (1.45)	2.08 (1.19)	0.67 (0.19)

4.4.2 Camera trap data

Records of average number of pictures for each species per camera trap day over time for each plot were simplified into average number of pictures for each species per camera trap day, night and day & night for pre-fire and post-fire sampling periods. Due to lack in pre-fire EDS data, the number of camera pictures was compared between all pre-fire and all post-fire data, regardless of season. This is justified by the fact that the dung counts on the controls did not change much over the season (Figure 4.2) Although there was no significant differences in all measures of camera pictures (p>0.05), the data showed that all species used the plots more during the day post-fire (Figure 4.4). Impala use the plots more during the night, whereas wildebeest and zebra show no change in nocturnal activity under post-fire. This suggests that impala are utilizing burnt plots for reduced predation risk at night.



	Impala	Wildebeest	Zebra
🟪 Post-fire Night	0.77	0.23	0.43
🟩 Pre-fire Night	0.06	0.27	0.32
🟥 Post-fire Day	0.56	0.99	2.21
🟦 Pre-fire Day	0.19	0.29	1.46

Figure 4.4 Comparison of number of camera pictures (nr pics/day &night;) for impala, wildebeest and zebra between pre- and post-fire sampling regardless of season.

Fire season

Sampling period/time had no significant effect on EDS number of camera pictures/day and night (Wilks = 0.90, F(3,15)= 0.63, p= 0.85), camera pictures/day and camera pictures/night (Wilks = 0.94, F(2,10) = 0.55, p = 0.085). Zebra was the only species to show a significant increase in the number of camera pictures/night between pre-fire April and post-fire July (p =0.04).

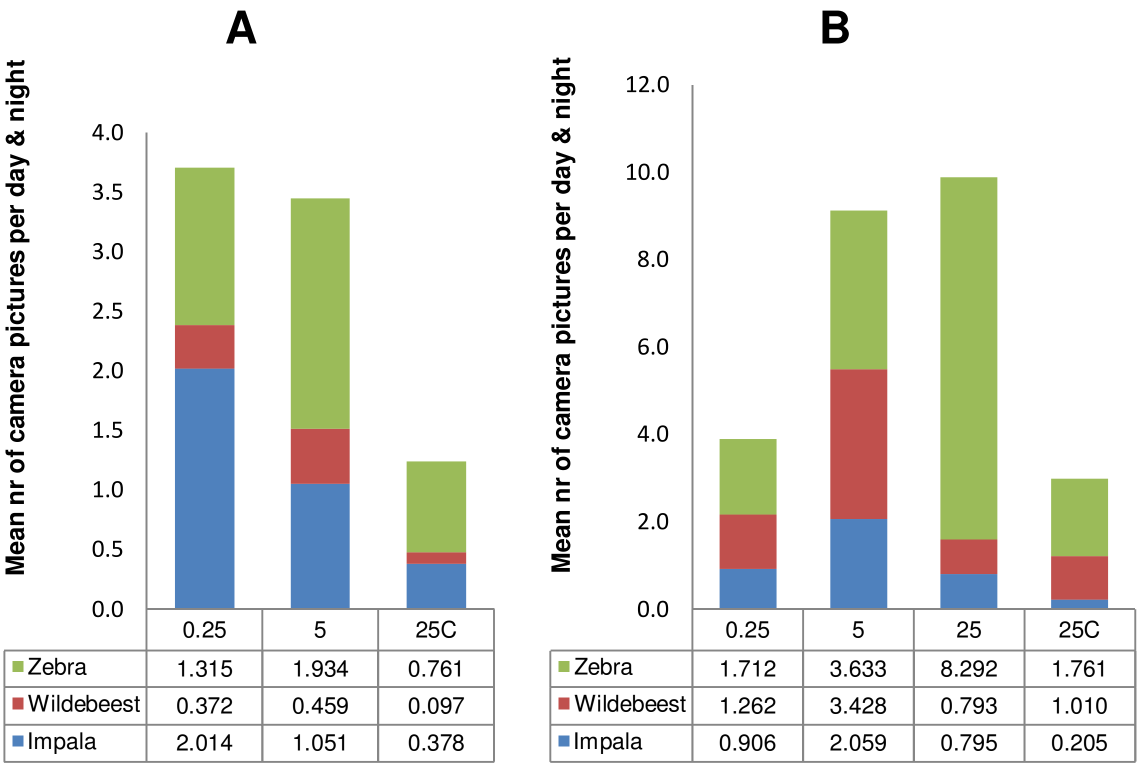
Sampling period had a significant effect on LDS number of camera pictures/day and night (Wilks = 0.80, F(3,12)= 1.82, p= 0.045), camera pictures/day and camera pictures/night (Wilks = 0.83, F(2,8) = 2.32, p = 0.02). Camera pictures/night increased significantly between pre-fire August and post-fire November (p=0.045) and from post-fire October to November (p=0.02). These increases were however not reflected on a species level with all three species showing no significant changes in the number of camera pictures/day (results from Tukey HSD, p >0.05).

Sampling period had a significant effect on control number of camera pictures/day and night (Wilks = 0.48, F(3,24) = 1.73, p = 0.03) but no significant effect no number of camera pictures/day and camera pictures/night (Wilks = 0.66, F(2,16) = 1.42). Impala was the only species to show a significant difference in number of camera pictures/day and night, pictures/day and pictures/night between post-fire June and post-fire May, June, July, September, October, November, December and January (p>0.05) with June having the highest recording camera pictures.

When pre and post-fire number of camera pictures per season was compared, trends in the data showed that impala use EDS and LDS plots equally, wildebeest use LDS plots slightly more post-fire than EDS plots, and zebra show higher use during EDS pre-fire than LDS, and higher use post-fire during LDS than EDS. These trends were reflected per sampling (over time). Number of pictures/day during LDS for zebra was significantly higher than that of impala (F(2,132) = 2.91, p = 0.04).

Fire size

There was no significant difference in number of camera pictures for wildebeest and impala for both EDS and LDS plot sizes (p>0.05). Zebra however showed a significant preference for 25 ha LDS treatment plots (F(3,67) =3.902, p=0.014) (Figure 4.5B). Impala, wildebeest and zebra were least photographed on control plots (Figure 4.5A & 4.5B). Wildebeest were most frequently recorded on the intermediate size treatment plot and impala were most frequently recorded on 0.25 ha and 5 ha treatment plots for both EDS and LDS (Figure 4.5A & 4.5B).



A

	0.25	5	25C
🟩 Zebra	1.315	1.934	0.761
🟥 Wildebeest	0.372	0.459	0.097
🟦 Impala	2.014	1.051	0.378

B

	0.25	5	25	25C
🟩 Zebra	1.712	3.633	8.292	1.761
🟥 Wildebeest	1.262	3.428	0.793	1.010
🟦 Impala	0.906	2.059	0.795	0.205

Figure 4.5 EDS (A) and LDS (B) mean number of camera pictures per day and night of all three species (impala, wildebeest and zebra) per plot size.

4.4.3 Animal behaviour

Vigilant, grazing and walking consisted of the highest proportion of behavioural activities, with grooming, resting/lying down and browsing being the lowest proportion (Figure 4.6).

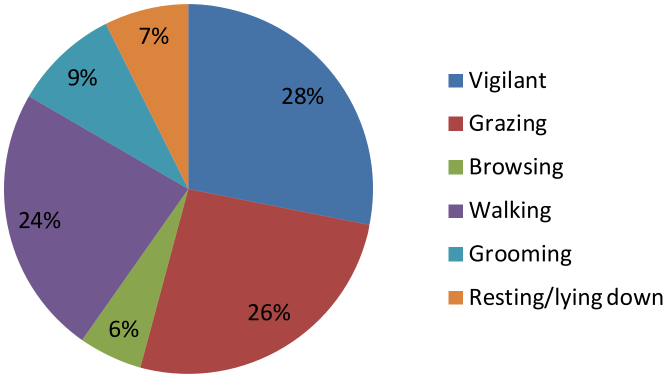


Figure 4.6 Graphic representation of proportions of behavioural activities recorded during animal observations.

Fire season

Proportion of animals vigilant (for all three species) decreased post-fire, however this was not significant (Figure 4.7). Proportion of impala and zebra grazing post-fire increased significantly (F(5, 9) = 342.30, p=0.019), whereas proportion of wildebeest grazing remained relatively unchanged from pre-fire conditions.

The proportion of animals grooming remains constant for all three species between pre- and post-fire periods. There was a significant difference in proportion grooming between all three species during post-fire sampling, with zebra having higher proportion grooming than impala (F(59)= 43.973, p=0.000) and wildebeest (F(59)= 43.973, p=0.000).

There is a significant difference in proportion resting/lying down between impala and wildebeest during post-fire sampling with wildebeest having higher proportion resting/lying down than impala (F(59)= 251.09, p =0.003). The proportion of animals resting/lying down is higher post-fire for zebra and especially wildebeest. Impala showed a decline in proportion of animals resting/lying down post-fire. This could be due to such an increase in proportion of animals grazing.

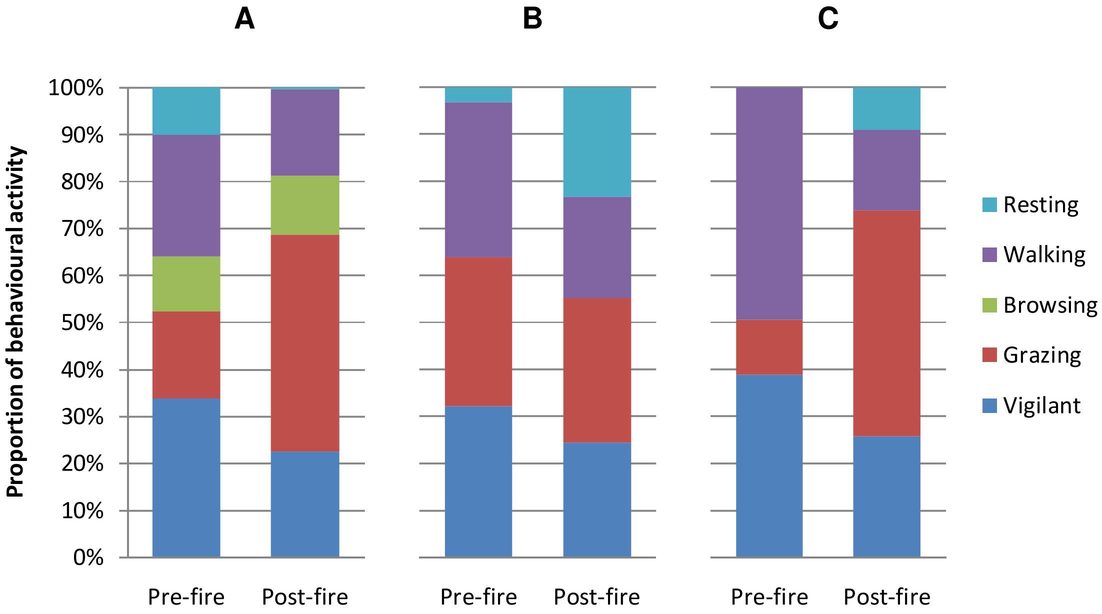


Figure 4.7 Graph representing behavioural activities for impala (A), wildebeest (B) and zebra (C) during pre and post-fire sampling.

<u>Fire size</u>

For EDS fires, there were no significant differences between all plot sizes (0.25 ha, 5 ha and control) in the proportion of animals vigilant (impala (F(1,8)= 0.14, p= 0.72), wildebeest (F(2,6)= 0.26, p=0.78), zebra (F(2,7)= 8.48, p = 0.06) and grazing (impala (F(1,8)= 4.35, p= 0.07), wildebeest (F(2,6)= 0.04, p = 0.96), zebra (F(2,7)=4.07, p= 0.07) for all three species. In regards to proportion grazing, wildebeest spent a higher proportion of time grazing on treatment plots (0.25 ha and 5 ha) than on controls. Zebra tended to spend more time grazing on 5 ha treatment plots than on 0.25 ha treatment plots and controls. This suggests that wildebeest prefer burnt to un-burnt areas and zebra have a preference for 5 ha treatment plots. In regards to vigilance, zebra showed highest proportion of vigilance on 0.25 ha plots and lowest vigilance on 5 ha plots.

On the LDS fires impala and zebra show no significant difference in the time spent on vigilance (impala (F(3,8)= 2.78, p=0.11), zebra (F(3,8)= 0.34, p= 0.80)) and grazing (impala (F(3,8)= 1.83, p= 0.22), zebra (F(3,8)= 0.36, p= 0.78)) in any plot size (0.25 ha, 5 ha, 25 ha and control). However wildebeest were significantly more vigilant on controls than on 25 ha treatment plots (F(3,8) = 5.166, p=0.03) (Figure 4.8). For all three species the following trend was shown: highest proportion of vigilance occurred on controls and the highest proportion of grazing occurred on treatment plots with impala showed a preference for grazing on 25 ha treatment plots.

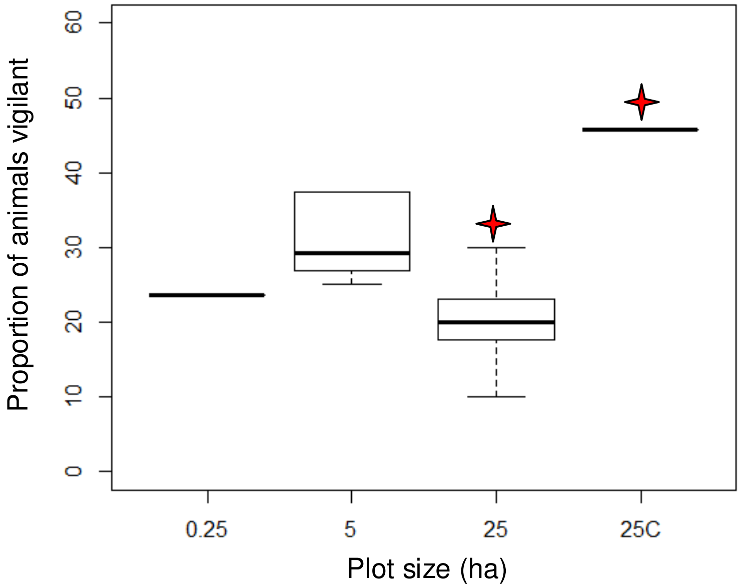


Figure 4.8 Proportion of wildebeest vigilant during LDS sampling across plot size. Star symbols represent a significant difference in proportion animals vigilant between plot size and control (25C)

4.4.4 Impala use of burnt areas – graze vs. browse

There was no significant difference in the proportion of impala grazing (Section 4.4.3), browsing (F(3,18) = 3.18, p= 0.05)between plot sizes. There appears to be a higher proportion of grazing than browsing on treatment plots, and a higher proportion of browsing than grazing on control plots, however these results are not significant (p>0.05).

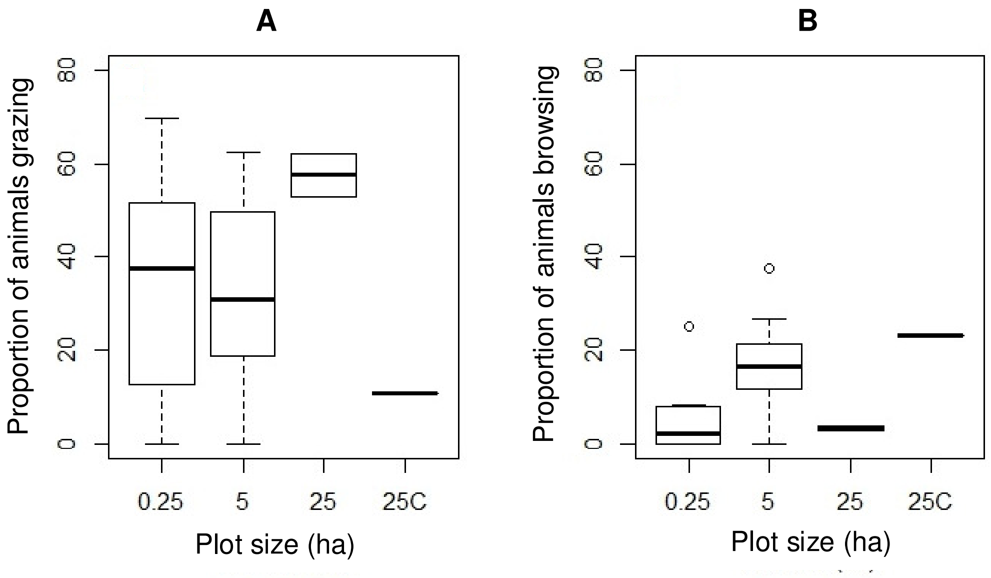


Figure 4.9 Proportion of impala grazing (A) compared to proportion of impala browsing (B) across plot size, under post-fire conditions.

4.4.5 Integration of results from Chapter 3 with results from Chapter 4

Dung vs. grass Height

Mean grass height under pre-fire, immediately post-fire and last sampling period were compared to the mean dung count of herbivore species (Table 4.3) to try show if species showed a preference for different grass heights (Table 4.1).

Table 4.3 Mean grass heights and mean dung counts of impala, wildebeest and zebra per sampling period for both EDS and LDS treatment plots.

Season	Sampling	Month	Mean Grass Height (cm)	Impala	Wildebeest	Zebra
Early	Pre-fire	April	56.59	0.16	0.50	0.75
Early	Post-fire	May	16.08	1.59	0.50	**3.72**
Early	Post-fire	June	14.33	2.25	0.72	2.13
Early	Post-fire	July	13.96	**4.19**	0.69	0.97
Early	Post-fire	December	11.79	3.91	**6.08**	**3.31**
Late	Pre-fire	August	38.15	2.29	1.15	1.92
Late	Post-fire	October	5.17	2.29	1.61	1.95
Late	Post-fire	November	8.06	**4.53**	**4.36**	1.72
Late	Post-fire	January	19.17	**4.23**	3.58	0.7

Impala mean dung count was highest at a wide range of mean grass heights from 8 to 19 cm (results highlighted in blue). Blue wildebeest mean dung count was highest when mean grass height was between 8-12 cm (results highlighted in red). Burchell's zebras' mean dung counts were highest when mean grass height was between 11 – 16 cm (results highlighted in green).

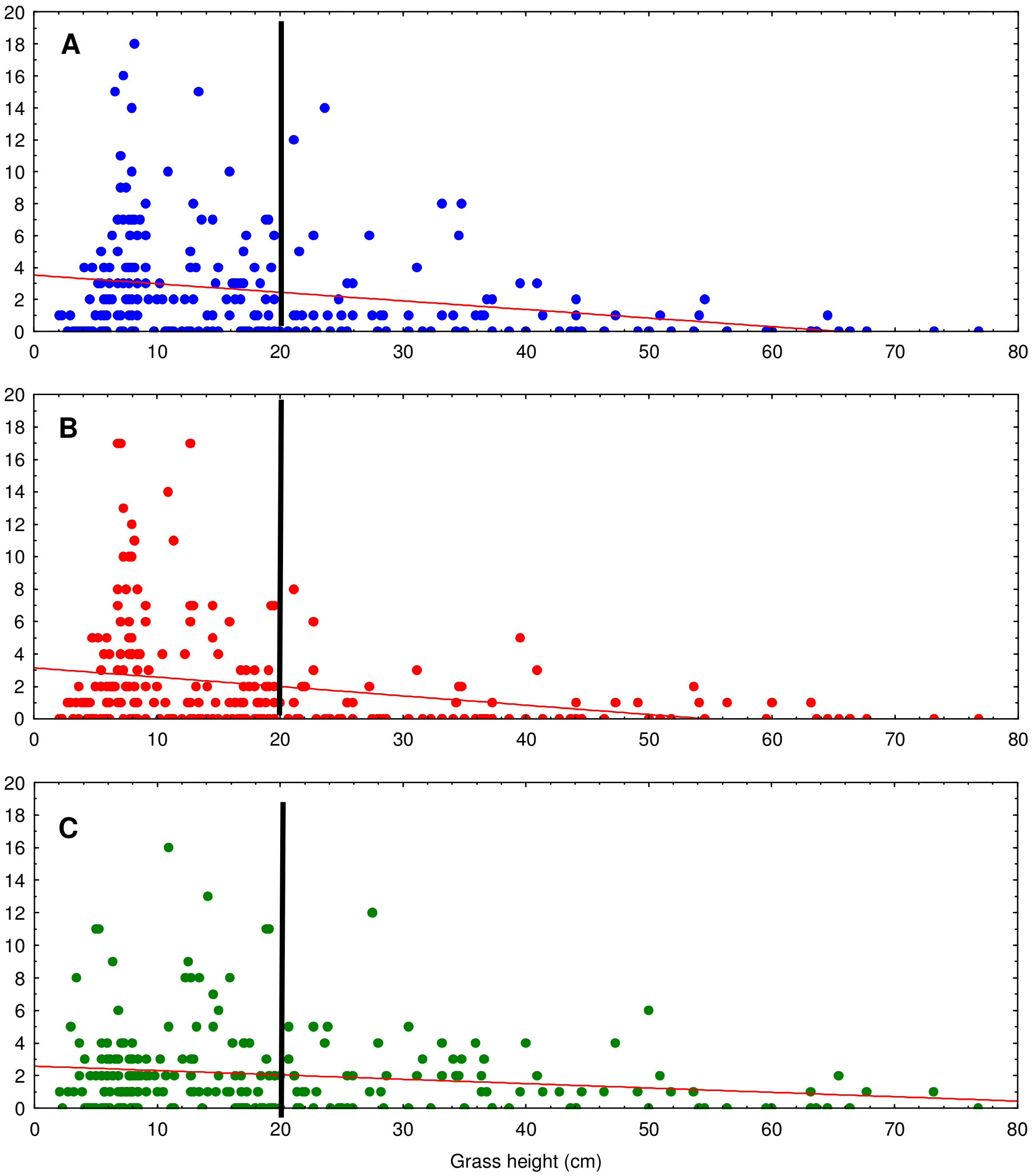


Figure 4.10 The number of observations of mean dung counts for impala (A) (r = -0.26), blue wildebeest (B) (r = -0.30) and Burchell's zebra (C)(r = -0.17)occurring on all treatment plots, regardless of sampling and season. The black line indicates grass height of 20 cm. The red lines indicate the linear regression.

Blue wildebeest mean dung counts were significantly higher (t= 2.59, df = 82, p=0.01) on plots with a mean grass height of less than 20 cm. Impala (t= 1.61, df = 54, p= 0.11) and zebra (t= 1.38, df = 54, p= 0.17) mean dung counts did not significantly differ between grass heights of more or less than 20 cm, however the majority of observations were recorded on plots that had a mean grass height of less than 20 cm (Table 4.3; Figure 4.10).

Visibility vs. vigilance and grazing

Portion of time spent vigilant and grazing, regardless of species was compared to visibility in the head down position per fire season and sampling period to determine if visibility did indeed impact animal behaviour. There was no significant difference between proportion of time spent vigilant compared to visibility (t = 0.28, df = 6, p =0.79) and grazing (t = 0.63, df =6, p =0.55) in the head down position. Although these results were not significant the data shows that when visibility was below 5 m, vigilance was high, especially under pre-fire conditions.

Table 4.4 Proportion of time spent vigilant (regardless of species) and grazing versus mean visibility in the head down position (0.3 m) per fire season and sampling period.

Season	**Sampling**	**Month**	**Time spent vigilant (%)**	**Time spent grazing (%)**	**Visibility at 0.3m**
Early	**Pre-fire**	March/April	**30.28**	**30.76**	**1.27**
Early	Post-fire	May	**20.39**	**51.82**	**4.90**
Early	Post-fire	June	**17.82**	**50.32**	**4.86**
Early	Post-fire	July	24.19	23.06	7.56
Early	Post-fire	November	23.53	38.97	5.02
Late	**Pre-fire**	August	**26.31**	**16.60**	**1.69**
Late	Post-fire	October	**22.33**	**19.48**	**13.77**
Late	Post-fire	November	**22.01**	**49.48**	**14.95**

4.4.6 Environmental factors and herbivore presence

Dung count data showed that the majority of plots (17/21) had a low dung count between 0-3 total mean dung counts for all three species (impala, blue wildebeest and zebra). Not many plots with high dung counts (>3) were recorded (4/21) (Figure 4.11).

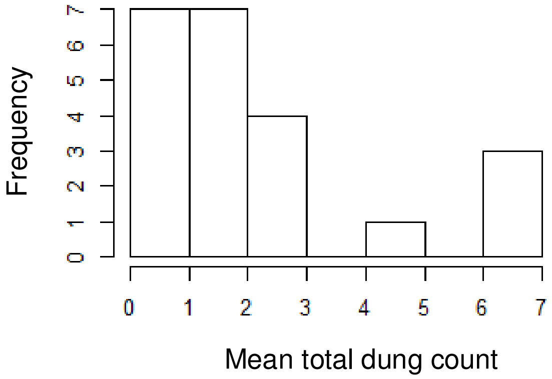


Figure 4.11 Distribution of total dung data under pre-fire conditions.

There was a non-significant, weak, and negative correlation (r^2 = -0.37) between distance to water and mean pre-fire dung counts for all plots (Figure 4.12A). There was no significant correlation (r^2= -0.06) between mean pre-fire forb percentage and mean pre-fire dung counts (Figure 4.12B) There was a weak positive correlation (r^2 = 0.26) between tree density and mean pre-fire dung counts (Figure 4.12C)

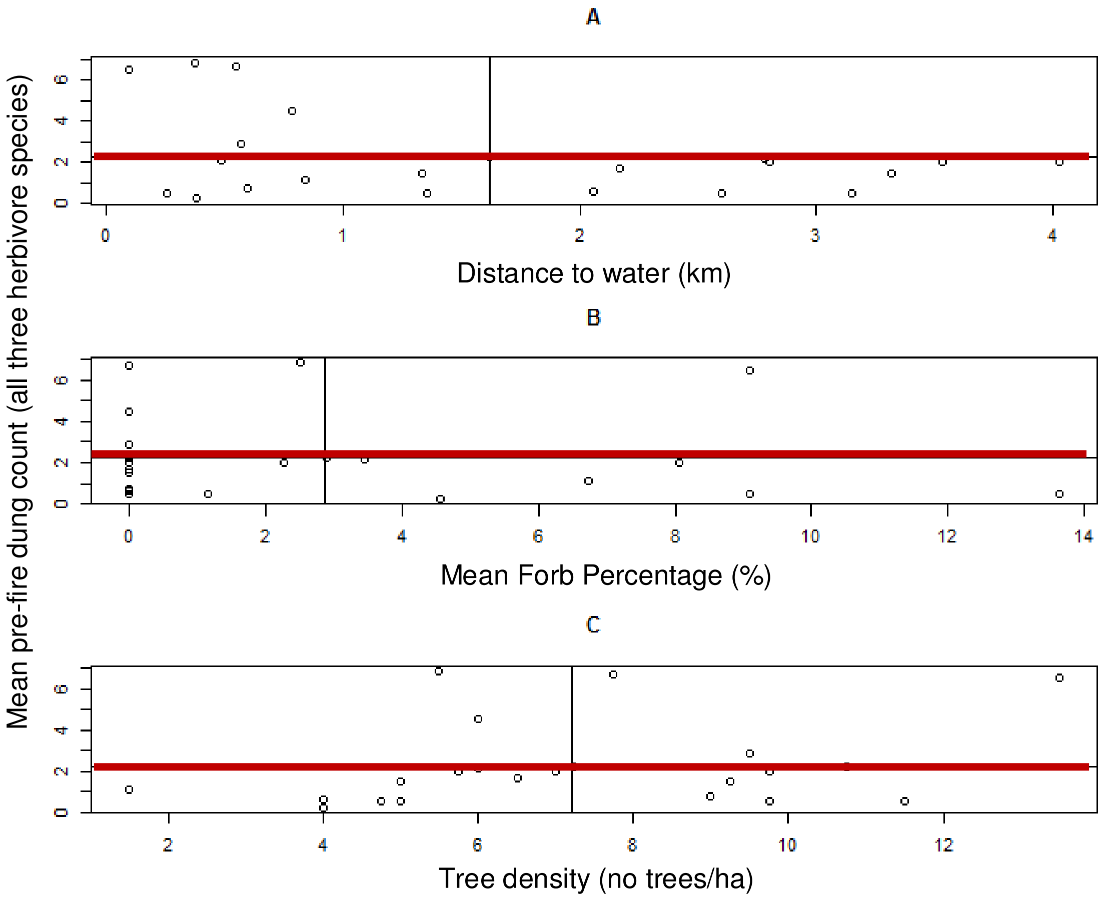


Figure 4.12 Correlation of total dung counts for all three herbivore species (impala, wildebeest and zebra): (A) distance to water (km), (B) mean forb percentage (%) and (C) tree density (no trees/ha), regardless of plot size or season. The horizontal solid red line represents the mean pre-fire dung count (3.78), and the vertical soil black line represents the average value of each of the environmental factors respectfully.

There was no significant difference in the mean pre-fire dung between plots that were more or less than 2 km from water (t = 1.57, df = 19, p = 0.133) (Figure 4.13A), plots that had a higher or lower forb percentage of 3 %(t =0.59, df=19, p = 0.56) (Figure 4.13B), and plots that had a higher or lower tree density of 7 trees/ha (t = -0.17, df = 19, p =0.87) (Figure 4.13C).

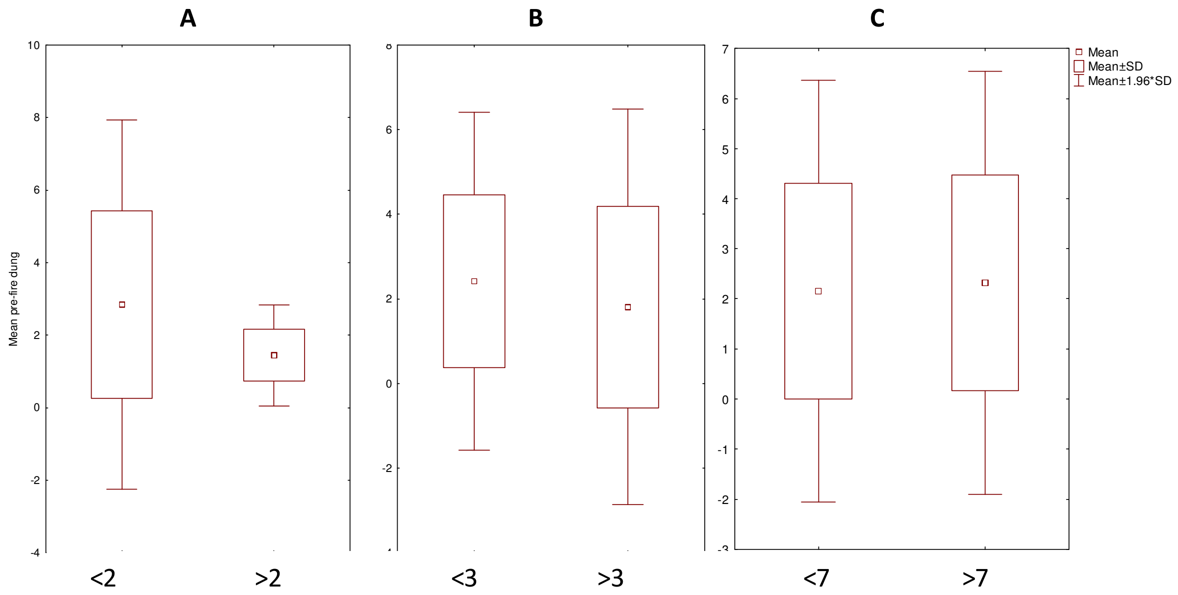


Figure 4.13 Mean pre-fire dung counts of plots less and more than 2 km to water (A), plots with less and more than a mean forb percentage of three (%) (B) and plots with less and more than a tree density of 7 (no trees/ha) (C).

4.5 Discussion

General results will be discussed, however due to the complexity of the above results in regards to differing methodologies yielding conflicting results, results will also be discussed per species in terms of how fire size and season impacts each species and consequently which factors (resource quantity, resource quality or predation risk) seem to be the main driving force behind the use of burnt areas.

Dung count results determined that all plots were used equally by all three herbivore species for both seasons under pre-fire conditions. Dung counts did increase post-fire for all three herbivore species in both seasons, however not all these increases were significant (Figure 4.2) and the response was not immediate (except for zebra in the early season). There was no sign that the herbivores were moving back off the burn plots by the end of the sampling season even though Chapter 3 shows that the nitrogen levels had declined to pre-fire levels of quality (Figure 3.9), and visibility in the head down position had also returned to the same levels as under pre-fire conditions (Figure 3.4). However, Chapter 3 also showed that grass biomass was still consistently lower than before the application of the burns (Figure 3.6), so a structural change was still apparent which might have been driving this behaviour.

After the burns, the larger and intermediate plot sizes seemed to be utilized more than the small plots. This could be due to the fact that 0.25 ha treatment plots are too small in regards to having lower forage quantity and higher predation risk due to lower visibility (smaller plots had a lower visibility and forage quantity than larger plots which had a higher visibility and forage quantity (Chapter 3)).

Camera trap results showed that there was an increase in the use of treatment plots post-fire, however this increase was not significant. There were no significant p values over time as well. More pictures per day and night were recorded on treatment plots than on controls, suggesting a preference for treatment plots by grazing herbivorous mammals. Trends in the data suggest that LDS treatment plots are used more than EDS treatment plots post-fire.

Animal behaviour data results showed clear changes in the following three behavioural activities for all three species; vigilance, grazing and resting/lying down, however these changes were not significant. Comparisons between seasons of herbivore behaviour showed no significant results.

4.5.1 Impala

Dung count data showed that neither fire size nor burn season impacted the use of plots. This suggested that resource quality is the dominant driving factor, as resource quality does not differ between plots (results from Chapter 3). Results from camera trap data showed that no preference for fire size or season, which again supports resource quality as the dominant driving factor for plot size selection. Impala showed a preference for burn plots over controls as the number of pictures per day increased post-fire (Figure 4.5). The number of pictures per night also increased after the burns, suggesting that safety or decreased predation risk was a driving factor. Impala are mostly diurnal (Rowe-Rowe, 1994) suggesting they are more likely resting than feeding at night. Impala showed a preference to larger burn plot sizes post-fire, which also supports decreased predation risk as a driver. Impala are known to observe predators and will flee only once the predator has entered into the impalas flight distance (Hunter & Skinner, 1998; Skinner & Chimimba, 2005), suggesting that higher visibility is very important and thus offering an explanation of why they remain in burnt areas longer than nutritionally beneficial. This is supported by my results, which show that impala spent more time in burnt areas than what was nutritionally beneficial (Table 4.3 and Figure 4.10A), and remained in burnt areas at times of the day when they do not normally feed (Hayward & Kerley, 2005; Kleynhans, E.J. et al*.,* 2010) (Figure 4.4). When looking at animal behavioural data, impala showed a clear, yet insignificant, increase in grazing and a decrease in vigilance under post-fire conditions (Figure 4.7A). This implies that the increased visibility in the head down position might be one of the key factors driving impala use of the burn plots. Interestingly, behavioural data also showed that impala, although mixed-feeders who can use both browse and graze resources, were in fact using treatment plots post-fire for grazing resources (Figure 4.9) Wilsey (1996) compared the use of burnt and unburnt areas for grazing for various ungulate species and found that impala showed a significantly higher use of burnt areas.

Impala show a preference for LDS 25 ha burnt areas, however their vigilance remained relatively constant regardless of plot size, which suggests that they were equally fearful of predators on the small (25 m to the edge) and large (250 m to the edge) burn plots.

4.5.2 Blue Wildebeest

Dung count data showed that wildebeest preferred EDS treatment plots post-fire than LDS treatment plots which showed no increase in dung over time. The increase of dung on EDS treatment plots only occurred towards the end of the sampling periods. This could possibly be due to grass height, with wildebeest showing a clear preference for grass heights of <10 cm (Figure 4.10) due to their mouth structure (Skinner & Chimimba, 2005). Camera trap data however showed a slight preference for LDS treatment plots (Figure 4.5B). This contradicts the dung data. Wildebeest did show a preference for burn plots and not controls as the number of pictures per day increased post-fire. Wildebeest showed a preference for the intermediate size treatment plots (5 ha) suggesting that resource quantity was the dominant driving factor of the use of burnt areas as resource quality was equal across plots. A study conducted in Kruger National Park by Smit (2011), determined that medium-sized herbivores, such as blue wildebeest, were driven by resource quantity when resource quality was at an acceptable level. However the same study states clearly that there are constant trade-offs between resource quality, quantity and predation risk (Smit, 2011). When looking at animal behavioural data, wildebeest showed decreased vigilance and increased resting/lying down behaviour under post fire conditions, but no increase in grazing. Wildebeest do not graze throughout the day (Skinner & Chimimba, 2005), thus no change in grazing but changes in other behaviour suggests that they were utilizing burn plots possibly for grazing but for safety as well (Figure 4.7).

4.5.3 Burchell’s Zebra

Dung count data showed that fire season has no impact on the use of burnt plots by zebra, with no significant increase in dung over time being recorded (Figure 4.2). Zebra however showed a preference for intermediate and large size burn plots suggesting resource quantity to be the driving force in zebra's of burnt areas with larger plots containing a higher biomass than smaller plot sizes (results from Chapter 3). Smit (2011) showed that zebra, in unburnt landscapes, were indeed driven by resource quantity due to their allometric scaling and digestive system (Hopcraft et al., 2010). Camera trap data supports this utilization of large and intermediate plot sizes and thus resource quantity as a driving force. Zebra did show a preference for burn plots and not controls as the number of pictures per day increased post-fire (Figure 4.5). When looking at animal behavioural data (Figure 4.7), zebra showed a clear increase in grazing and resting/lying down and a decrease in vigilance on burn plots under post-fire conditions. This suggests that both food (increased grazing) and safety (increased resting and decreased vigilance) are the dominant driving forces (Hopcraft et al., 2010).

4.5.4 Summary table of findings

The table below (Table 4.5) tries to represent the results discussed above in regards to each method and species.

Table 4.5 Summary of findings from results achieved.

Herbivore data used	**Species**	**Relative importance of driving factors (resource quality, quantity and predation risk)**
Herbivore presence (dung)	Impala	LDS: Resource quantity> resource quality and predation risk EDS: Predation risk and resource quantity > resource quality
	Wildebeest	LDS: Resource quantity > resource quality and predation risk EDS: Predation risk and resource quantity > resource quality
	Zebra	LDS: Resource quantity > resource quality and predation risk EDS: Predation risk and resource quantity > resource quality
Herbivore behaviour	Impala	Predation risk > Resource quality and quantity
	Wildebeest	Predation risk > resource quantity and quality
	Zebra	Resource quantity > predation risk > resource quality
Camera trap data	Impala	Predation risk > resource quantity and quality
	Wildebeest	Resource quantity and quality > predation risk
	Zebra	Resource quantity and quality > predation risk

There is no significant evidence that plots closer to water had higher herbivore use, but due to the fact that plots were located near to water (within 4 km) in the study site these results can be biased as all animals had access to water (Figure 4.13A). Forb percentage showed that herbivores had no significant preference for plots with a higher or lower average forb percentage of 7 % (Figure 4.13B). The majority of the study site plots showed a low mean forb percentage. This can be due to the fact that the forb species which were present on the plots could have a low nutritional value or herbivores were not actively selecting forbs but were more focussed on the grass resources. Tree density showed that herbivores concentrated on plots with an intermediate tree density (Figure 4.13C). The majority of the study site plots had an intermediate tree density. Tree density impacts visibly, thus one would expect herbivore to occur in areas with a lower tree density in order to reduce predation risk, why then concentrate on areas with an intermediate tree density and subsequent higher predation risk? This could be due to the different grass species occurring at the base of trees offering higher nutritional content at certain times of the year, or due to the presence of shade, allowing animals to stay on plots during the hottest times of the day (Burkepile et al., 2013).

4.6 Conclusion

What is clear from the data presented in this chapter is that first, herbivores do make use of the post-fire environment as much literature has indicated, and secondly fire size influences herbivore use with larger plots yielding higher forage quantity and visibility (Chapter 3) and possibly fire season impacting herbivore usage with data suggesting that herbivores are more driven by safety in EDS than food and vice versa for LDS.

Herbivores respond to the changes in the landscape stimulated by fire. There are many factors which determine why herbivores choose specific habitats all of which is driven by the herbivores needs. These needs are determined by body size and digestive system. Body size affects how much and what quality of food a herbivore needs as well as how susceptible it is to predation (Eby et al., 2014; Sensing et al., 2010). Small-bodied ruminant herbivores, such as impala, were predicted to be able to occur on all plot sizes due to forage quality driving their resource selection and did in fact occur on all plot sizes for both fire seasons (Figure 4.5). They also were found to occur on the larger plots more during the night, suggesting that they were there for safety and not food (Figure 4.4). Behavioural data showed that impala were less vigilant allowing them to graze more in the post-fire environment (Figure 4.7). Thus impala were using burn plots for both an increased forage quality (Figure 3.7) and visibility (Figure 3.4).

Medium-bodied ruminant herbivores, such as blue wildebeest, were predicted to be driven by both food and safety and our data confirmed this. Wildebeest were less vigilant on burn plots however they did not increase their grazing activity (Figure 4.7). This is due to wildebeest showing a significant preference for short grass (Figure 4.10) under post-fire conditions. This explains why wildebeest presence did not increase immediately post-fire but only from December for EDS burns (mean grass height of 11.79 cm) and November for LDS burns (mean grass height of 8.06 cm) (Table 4.3) (Figure 4.2) although this increase was not significant ($p>0.05$).

Medium-Large-bodied non-ruminant herbivores, such as Burchell's zebra, were predicted to be driven by forage quantity rather than quality or predation risk, thus using larger treatment plots more than smaller treatment plots (Figure 4.3; Figure 4.5) which offer less forage quantity (Table 3.2) under post-fire conditions. Zebras showed a clear preference for the post-fire environment (Figure 4.2, Figure 4.4), however this increased presence was more noticeable in EDS than LDS. This could be due to the fact that Zebra are less worried about predation due to their body size and thus willing to occur on plots with lower visibility.

Based on literature one would expect that the higher the visibility the lower the vigilance however there was no significant difference. Even though results from this were not significant (Table 4.4) the data shows that herbivores were more vigilant under pre-fire conditions when visibility was at its' lowest for both fire seasons and less vigilant under post-fire conditions when visibility was higher. In regards to grazing, due to a higher visibility herbivores should feel safer to graze. Mean proportion of time spent grazing, was at its lowest for both seasons under pre-fire conditions and higher under post-fire conditions. However these results were not significant (Table 4.4). There was also no significant difference between proportion of time spent vigilant between fire seasons for all three species which disproves the prediction made in Chapter 4 (Section 4.2). There was a significant increase in grazing post-fire for impala and zebra but not for wildebeest (Figure 4.7). Once again this can be attributed to wildebeests' preference for short grass heights (Figure 4.10; Table 4.3).

Environmental factors were examined in order to try and explain some of the results determined in Chapter 3 and 4. I found however that, in this case, and on a plot level, that distance to water, forb percentage and tree density did not significantly influence our measures of animal presence (mean dung counts per plot for all three herbivore species) (Chapter 4, Section 4.4.6). This justifies my decision not to include them as random effects in my model.

This chapter shows, that by using three different types of herbivore data and comparing different fire seasons and sizes, we can show how the relative importance of both resource quality and quantity and predation risk can impact herbivores of different body sizes to alter herbivore activities and habitat decisions.

5 CHAPTER 5: GENERAL CONCLUSION

The factors controlling herbivore habitat selection is an ongoing research question which has a broader importance for conservation authorities assessing the consequence of different management techniques as well as how these management techniques impact ecosystem drivers such as predation and fire. This study suggested that all three of the herbivores studied in a relatively high predator pressure environment (Pienaar, 1969; Smuts, 1978; Mills et al., 1995) were making habitat choices to reduce predation risk. These choices often concurrently allow for an increased forage intake rate (e.g. increased grazing and decreased vigilance behaviour in the post-fire environment). There were however some indications that two species, impala and wildebeest were making habitat selection for safety at the expense of forage quantity or quality.

With the data from my study it is impossible to determine if fires in savanna areas can reduce predation for herbivore populations, however I have shown that fire does provide forage which exceeds the minimal maintenance levels of nitrogen when this is unavailable in the landscape (Prins 1996). These results and effects are well documented in various other studies (Grant & Scholes, 2006; Van de Vijver et al, 1999). My study was particularly interested in the relative value of small vs large fires, and early vs late-season fires. Results from fire size were not conclusive – clearly larger fires provide more of the high-quality forage, so at short time scales it would be advantageous to herbivores to burn large sections of the landscape. However, my data show that small fires are at least as effective at attracting herbivores as large fires. Once again this implies that forage is not the only driving factor determining herbivore use of burnt areas. The fact that even small (50 m x 50 m) fires can attract grazing animals has implications for the use of fires to manipulate grazing activities and over time, potentially grass community states.

There were, as there are in all research projects, aspects of data collection techniques which needed adjustment as sampling progressed and which can be improved for future use in obtaining similar data. Dung counts, although more reliable than camera trap data or animal observation data (Figure 4.1), were highly influenced by the presence of rain and dung beetles. Limiting dung counts to transects often meant that mega-herbivores such as white rhinos were excluded from the data (Van Vleit et al., 2009; Bouche et al., 2012; Li et al., 2014). Camera trap data were very inconsistent due to technical issues with malfunctioning equipment, however the data we did get were very insightful in terms of what time of the day or night animals were utilising plots. The set up of the cameras was not systematic and locations were not decided before hand. More camera traps should be used to record the use of the total plot, not just a proportion of the plot. A time lapse camera trap would help to keep data consistent and would not be influenced by moving vegetation or insects draining batteries. Animal observation data was mostly collected in the afternoon, this excludes a large proportion of the day when animals are most active. Disturbances from passing vehicles as well as limited visibility from the edge of the plot also influenced the amount of sightings. I suggest that animal observation data should be collected separately as a full time data collection. Grass greenness was found to be a good indicator of landscape nitrogen levels however it does not reveal trends in nutritional quality of grass in the post-fire environment, and there was a wide range of grass total Nitrogen concentrations at 100% grass greenness (Figure 3.6), hence the use of grass sampling to determine total grass Nitrogen content, although costly, is recommended. Landscape level experiments are always difficult due to external factors being part of the system. Fires in nearby sections, fire breaks around experimental burn plots and camps could have influenced herbivore attraction, although from personal observations this did not seem to be a big factor as there was still relatively little fire in the surrounding landscape. Actual predator presence was not measured during this study period and would be hugely beneficial when looking at animal behavioural data and trying to explain the movement of herbivores based on perceived and actual predation risk.

A second aim of the experiment at Satara was to ascertain which fire management practices have the potential to not only attract but to keep herbivores in an area long enough to stimulate the formation of grazing lawns and my study emphasises the importance of fire season in this regard.

The results achieved in this thesis adds to the growing trend of viewing fire and herbivory as interacting disturbances (Fuhlendorf et al., 2009), which impacts the ecosystem in such a way that they cannot be studied independently. Here I demonstrate that the impact of fire on herbivory can be indirect – via its impacts on vegetation structure which in turn alters forage availability and quality as well as fear of predation, and might have longer-term impacts on herbivore demographics and grass community composition. My research lends weight to arguments for more integration between the goals of fire, herbivore, and predator management, something that is currently a priority for South African National Parks.

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Appendix 1: Map of study area