RESOURCE USE BY REINTRODUCED LARGE AFRICAN HERBIVORES IN AN ALTERED LANDSCAPE

by

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Abstract

Suitable habitat for large terrestrial animals is declining worldwide and protected areas provide viable habitat for these species. However, human disturbances can make potential habitat less suitable for species of concern, and can cause extirpation or even extinction. Gorongosa National Park in Mozambique experienced the loss of nearly all of its large grazing herbivores causing a shift from short, nutritious grasses to low-quality grass. The objectives of this study are twofold (1) to determine the drivers of resource selection by reintroduced blue wildebeest (*Connochaetes taurinus*) and African buffalo (*Synercus caffer*) to an altered system with low herbivore abundances and minimal risk of predation; (2) to identify the mechanisms by which these two species select resources on the patch scale by the creation of artificial grazing lawns. I performed AIC model selection on a suite of predictor variables to identify important factors driving resource selection on multiple spatial scales across three seasons. Next, I experimentally tested the effects of a mowing treatment on patch use by the two species to elucidate the interactions between grass clipping, soil and grass nutrients, and herbivore use. The findings of this study identify three major trends in resource selection by both species. First, wildebeest selected short, protein-rich grass patches during all seasons when available while buffalo utilized these patches predominantly during the early dry season when other resources are scarce. Second, open (low-tree cover) areas and proximity to water were secondary factors that determined wildebeest resource selection. Third, morphological adaptations allowed buffalo to feed on tall or short grasses depending on resource requirements; grass height was not a significant factor in resource selection. In the wet season, when resources were abundant, buffalo choice was driven by the composition of grass species. During the late dry season, buffalo chose unmowed salt plain vegetation in previously burned areas which had high percent grass greenness. These trends indicate that the establishment of short, productive grazing lawns would be highly beneficial for wildebeest during all seasons while a diversity of grass patch heights, grass species, vegetation types, and burning regimes would benefit buffalo.

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1 Introduction

1.1 Background

Suitable habitat for large mammals is decreasing globally due to human encroachment and habitat fragmentation (Shi *et al*. 2005). In many places throughout Africa and elsewhere, large mammal populations are restricted to protected areas of minimal human disturbance. It is important to understand the underlying drivers of resource selection to better understand local ecology and to inform conservation decisions.

Resource use by animals is defined by environmental factors and community interactions (Begon *et al*. 2006). The basic factors that shape resource use by herbivores are food resources, water resources, shelter and physical barriers (Sinclair 1977, Begon *et al*. 2006). Herbivores must be morphologically adapted to ingest and digest food and those food resources must be in an area that is physically accessible (McNaughton and Georgiadis 1986, Hofmann 1989). Forage must be of high nutritional value for the energy gained in consuming it to outweigh the energy costs of locating, ingesting, and digesting it (Penneycuick 1979). In cases where the nutritional value of the food is too low, the animal's physical condition will deteriorate (Sinclair 1977). Water sources must be physically accessible and within a minimum distance to other essential resources, such as grazing areas or shelter (Western 1975, Redfern *et al*. 2003). Shelter can provide protection from extreme elements and a refuge from predators (Mysterud and Østbye 1999).

Community interactions can limit or extend suitable habitat through competition, facilitation, and predation (Begon *et al*. 2006, Morin 2011). Human habitation represents one form of competition where the modification of habitat by humans or the presence of humans alone renders some habitat unsuitable for an animal (Prins 1992, Apps *et al*. 2004). Facilitation occurs in herbivory where a herbivore species grazes tall grass thereby providing access to shorter grass that is favorable for another species (Vesey-Fitzgerald

1960). Predator density can affect distribution patterns of prey species as they select habitat for predator avoidance or visibility (Jarman and Sinclair 1979).

Patterns of herbivore resource use can vary depending on spatial and temporal scale (Morris 1987). Animal distributions could be driven by landscape-scale factors such as water availability while daily movements could be driven by patch-scale factors such as plant height. Resource use may also vary temporally as resource availability changes across seasons. Herbivores can impact the environment in a variety of ways producing short-term or long-term changes to resources. Herbivores directly affect plant structure by feeding on plant parts thereby reducing plant biomass and/or height (Stobbs 1973). Large-scale biomass reduction limits fuel availability thereby reducing fire frequency (Savadogo *et al*. 2007). Changes in fire patterns can have a myriad of effects including changes in woody vegetation, soil properties, and animal distributions (Dublin 1995, Govender *et al*. 2006). Moderate levels of defoliation can initiate compensatory regrowth of nutritious plant shoots while overgrazing can have detrimental effects on plant regrowth (McNaughton 1979a, 1979b, Trlica 1993, Hobbs 1996). Herbivores input nutrients to the soil that influence plant productivity and nutrient availability (Ruess 1984, Ruess and McNaughton 1987, Jaramillo and Detling 1988, Day and Detling 1990, Hobbs 1996). Feeding patterns can influence long-term changes in plant species composition (McNaughton 1978, McNaughton 1979a). Herbivores may preferentially use areas where an environmental disturbance has shifted the state of the ecosystem. An alternative stable state is then created when herbivores maintain the environment in this state (Beisner *et al*. 2003).

1.2 Wildebeest and buffalo ecology

Blue wildebeest (*Connochaetes taurinus*) and African buffalo (*Synercus caffer*) are ungulates of the family Bovidae that are also classified as ruminants, as they can break down cellulose in their rumen before passing food to their gut (Hofmann 1978, Estes 1991). Wildebeest belong to the tribe Alcelaphini while buffalo belong to the tribe Bovini (Estes 1991). The distribution of wildebeest extends from East Africa to the northern regions of South Africa; they are absent from wet savannas and rainforests of central

Africa (Estes 1991). Buffalo are distributed across most of Sub-Saharan Africa in many vegetation types including dense rainforest, montane forest, grassland and savanna (Sinclair 1977).

Wildebeest and buffalo are both predominantly grazers, although buffalo will selectively browse, especially when grass resources are scarce (Sinclair 1977, Estes 1991). Wildebeest are bulk grazers whose wide muzzle, loose lips, and wide row of incisors are well adapted for clipping short grass below 5cm in height (Estes 1991). Buffalo are also bulk grazers whose prehensile tongue and large molars make them well suited for ingesting and grinding tall, coarse grass (Estes 1991). Their wide muzzle provides the option to feed on short grass but their stiff lips prohibit them from reaching short grass below 5cm in height that wildebeest prefer (Estes 1991). Buffalo prefer to feed on grass between 5cm - 80cm in height where available (Grunow 1980).

Fine-scale grazing selection can occur on the level of grass species when herbivores select favorable species on the basis of nutrient quality and palatability (Augustine and McNaughton 1998). Wildebeest select short-growing grass species that exhibit compensatory growth in response to grazing (Estes 1991). Buffalo select tall grass species and species with high protein and carbohydrate content (Sinclair 1977, Prins 1996). Important plant nutrients for both species include grass protein (nitrogen), carbohydrates, phosphorous, and sodium (Sinclair 1977, Murray 1995, Prins 1996, Prins and Beekman 2008).

Wildebeest and buffalo are both considered water-dependent herbivores that must drink a minimum of once every 1-2 days (Sinclair 1977, Estes 1991, Prins 1996). Wildebeest are estimated to consume an average of 2.99 liters water/100 kg body weight/day while buffalo consume an estimated 3.43 liters water/100 kg body weight/day, including water obtained from food (Taylor 1968). Due to their dependence on water, resident wildebeest rarely move more than 15km from a water source and buffalo generally remain within 5km of water (Redfern *et al.* 2003) but are known to travel up to 30km in a day in search of food and water (Sinclair 1977). The amount of water consumed and distance traveled to find water can vary dramatically between seasons (Redfern *et al.* 2003).

In addition to food, suitable habitat must provide shelter from elements and from predators. For wildebeest, predator visibility is of primary importance as they are commonly preyed upon by lions and other large predators (Smuts 1978, Estes 1991). Wildebeest, therefore, prefer open areas with few trees for optimal visibility (Estes 1991). Buffalo, in contrast, use shaded areas of thick savanna and woodland during the day to provide shade from the sun (Sinclair 1977). Buffalo herds are less vulnerable to attacks from lions than wildebeest and they have been reported to effectively mob-attack their predators to defend herd members (Estes 1991).

In the Serengeti ecosystem, wildebeest and buffalo compete for food in specific vegetation types, such as riverine grassland, but their habitats do not completely overlap as wildebeest generally prefer open savanna and buffalo prefer woodland (Sinclair 1977, Jarman and Sinclair 1979). If competition among herbivore species exists, it is generally most pronounced during the dry season months when resources are scarce.

Species are adapted to fill ecosystem niches, and this phenomenon is evident in the widely-studied savanna grazing succession (Vesey-Fitzgerald 1960, Bell 1971). In this process, grazing by one species facilitates the next in a chain that can substantially modify the ecosystem -- elephants trample tall grass, creating access for buffalo to graze the grass to a medium height. Zebra follow by grazing grass to shorter heights suitable for wildebeest and smaller antelope (Vesey-Fitzgerald 1960, Bell 1971). These highly productive “grazing lawns” can be maintained in a short grass state with sufficient and consistent grazing (McNaughton 1979a, 1984).

1.3 Study area

The 3970 km² Gorongosa National Park (hereafter “Gorongosa”) is located in central Mozambique at the southern tip of the African Rift Valley. The park's heterogeneous landscape is comprised of vegetation types ranging from lowland floodplain grassland to montane rainforest interspersed with savanna and woodland (Tinley 1977). The Gorongosa ecosystem receives an average of 800 - 1000mm of rain annually (Tinley 1977) with the wet season months (December – March) experiencing a majority of the rainfall. It is not uncommon for a short rainy period of one to two weeks to occur in June or July (*pers. obs*.). High annual rainfall, coupled with heterogeneous soil types are the foundation for Gorongosa's highly productive and diverse ecosystem.

During the 1960s and 1970s, Gorongosa was renowned for supporting large and diverse wildlife populations. The triad of large grazing herbivores reached population levels of 14,000 buffalo, 3,300 zebra, and 5,500 wildebeest in 1972 (Tinley 1977). The grassland and savanna grasses were kept short by the park's abundant herbivores (Tinley 1977). By the end of Mozambique's civil war in 1992, populations of herbivores had been reduced to an estimated 50 buffalo, 30 zebra, and 5 wildebeest in 2006 (Anderson *et al*. 2006). The near-extirpation of the park's large grazers allowed the once short, productive grasses to overgrow, reaching average heights of 1 – 2 meters (*pers*. *obs*.). Every dry season, large quantities of dry grass act as fuel for uncontrolled wildfires (*pers*. *obs*.). A large-scale wildlife reintroduction effort is currently underway to restore the wildlife populations to a viable level (Anderson *et al*. 2006). Between 2006 and 2009, 85 buffalo and 180 wildebeest were relocated to a 62 km² fenced wildlife sanctuary within the park.

Gorongosa's wildlife sanctuary is comprised of four broad vegetation types, floodplain grassland at low elevations, savanna and salt plain (i.e. sodic savanna) at moderate elevations, and miombo woodland at the highest elevations. The sanctuary has abundant water during the wet season but no naturally occurring perennial water sources. Park management built a dammed reservoir and a number of boreholes throughout the sanctuary to meet the dry season water requirements of the sanctuary wildlife. Controlled patch burning occurs during the early dry season to reduce grass fuel and to provide wildlife with refuges if wildfires occur late in the dry season.

1.4 Objectives

The overall objective of this study was to understand the environmental mechanisms underlying resource selection by wildebeest and buffalo when herbivore abundances are low and risk of predation is minimal. This question is important for understanding the resource requirements that determine habitat suitability for species of high conservation priority, and thus for assessing the suitability of potential reintroduction sites in the future.

In chapter one, I used model selection to identify the factors that determined wildebeest and buffalo resource selection throughout three seasons. I also determined whether these two species selected similar resources in each of the three seasons. In chapter two, I experimentally tested how grass mowing affected soil and vegetation properties in grass patches to determine how these properties affected patch selection by wildebeest and buffalo.

1.5 Conservation implications

This study identifies patterns in resource selection by two important grazing species. This will allow managers to identify and protect suitable habitat, quantify resource availability, and predict future population distributions and seasonal movements. This study also serves as a baseline study to compare the effects of future herbivore reintroductions and subsequent population growth on the environment.

Understanding the environmental mechanisms underlying resource selection will provide researchers with a foundation to support future studies on drivers and limits to population growth and the effects of predation and competition on resource selection. Future studies may also investigate the processes underlying the formation and maintenance of an alternative grassland state.

2 Seasonal resource selection by reintroduced large African herbivores in a heterogeneous landscape

2.1 Introduction

2.1.1 Importance of understanding resource selection

The decisions through which animals select food and habitat (resource selection) are nearly-ubiquitous ecological processes through which individuals maximize fitness. As such, resource selection links the behavior of individuals to a host of broader population-level phenomena, including rates of population change, the relative magnitude of top-down versus bottom-up control, and species distributions across regions (Brown *et al.* 1995, Manly *et al.* 2002, Bowler and Benton 2005). Studies on resource selection can illuminate resource preferences (or requirements) for species or populations of conservation concern, thereby informing restoration efforts, reserve design, and predicted responses of animals to climate change (Martin 2001, Johnson *et al.* 2004, Cañadas *et al.* 2005).

The Gorongosa Restoration Project in Gorongosa National Park, Mozambique, offers a controlled – and therefore unusual – opportunity through which to explore resource selection of two experimental populations of reintroduced herbivores, thereby providing information to guide future reintroduction efforts. Between 2006 and 2009, 85 African buffalo (*Synercus caffer*) and 180 blue wildebeest (*Connochaetes taurinus*) were reintroduced into a predator-proof sanctuary within Gorongosa National Park, a protected area from which they had nearly been extirpated during the previous decade. To my knowledge, this is the first study to examine resource selection of large, reintroduced herbivores to an area with minimal risk of predation and very low abundances of other herbivores. This setting provides a lens for how these two widespread and ecologically-important grazers (McNaughton 1984, Prins 1996, Van de Koppel and Prins 1998) respond to spatial and temporal heterogeneity where predation and competition are ostensibly low.

2.1.2 Problem statement

Wildlife habitat is decreasing worldwide at an accelerating rate as the world's human population increases (Shi *et al*. 2005). Bulk grazers require large areas with sufficient resources to sustain them (Linstedt *et al*. 1986, Boshoff *et al*. 2001). Conservation of protected areas is vital to maintain wild animal populations. Relocation of animals from protected areas with an overabundance of animals to protected areas with low densities of animals is becoming increasingly common to offset the decline in local wildlife populations.

Gorongosa National Park in Mozambique (hereafter "Gorongosa") is an area where many all of the large grazing herbivores were nearly extirpated as a result of civil conflict two decades ago (Anderson *et al*. 2006). The reduction of these herbivore populations resulted in the overgrowth of grass in this highly productive landscape, providing fuel for wildfires each dry season. A large scale reintroduction program is underway to restore large herbivores and subsequently maintain grass overgrowth (Anderson *et al*. 2006). Historic studies of wildlife in Gorongosa prior to the mass reduction of herbivores showed that park resources were capable of sustaining highly diverse and abundant herbivore species (Tinley 1977). Prior to the civil war, Gorongosa was home to 42 species of mammals (≥ 5kg) with its productive grasslands supporting high densities of grazers including 14,000 buffalo, 5,500 wildebeest, 3,300 zebra and 3,500 hippo (Tinley 1977).

Currently, it is unknown how grass height and wildfires influence resource selection by two reintroduced herbivores (buffalo and wildebeest). Understanding how burning and grass clipping (as a surrogate for grazing under higher densities of herbivores) affects resource selection of these species will provide important information about the response of these species to natural or artificial habitat modification, and thus inform future management decisions.

2.1.3 Objectives and predictions

The overall objective of this study was to identify the important environmental factors that determined buffalo and wildebeest resource selection across three seasons: wet season, early dry season, and late dry season. A set of models were constructed *a priori* and grouped into seven categories that represent broad environmental drivers of resource selection: forage quality, forage quantity, forage value (i.e. forage quality and quantity combined), forage type, abiotic factors, forage value with abiotic factors, and broad scale factors (i.e. vegetation type, and burned vs. unburned areas). The objectives of this study were threefold: (1) To determine which of these categories best explained resource selection by each species during the three seasons. (2) To examine the important variables within the selected models and their relationships with species abundance. (3) To determine whether the two herbivores selected similar resources during the three seasons.

I predicted that buffalo and wildebeest would use habitat close to water during the early and late dry seasons because water is a limiting factor for African herbivores in the dry months (Western 1975, Sinclair 1977). I predicted that buffalo would use areas with high grass quality during the dry seasons and wildebeest would utilize this resource during all seasons because wildebeest have been shown to take advantage of areas of green flush in search of high quality forage year-round (Wilmhurst *et al*. 1999) while buffalo seek out this resource predominantly during dry months when resources are scarce (Sinclair 1977, Prins 1996). I predicted that buffalo would use areas of tall grass during all seasons because studies have shown that they feed on taller grass than many other grazers (Sinclair 1977, Prins 1996). I predicted that buffalo would use floodplain grass communities during the dry seasons because these low-elevation areas remain wet and green longest during the dry season and buffalo are adapted to feed on the tall floodplain grasses (Estes 1991). I predicted that wildebeest would use salt plain habitats and areas with short grass during all seasons because wildebeest are well adapted to graze on short grass (Estes 1991) and the nutrient rich grasses of sodic savannas are attractive to herbivores (Grant and Scholes 2006).

I predicted that resource selection of wildebeest and buffalo would be similar during the dry seasons as distance to water and forage quality would assume the greatest importance of all habitat predictors for both species. I predicted that, following the rains, buffalo and wildebeest would display differential use of grass species, vegetation type, and vegetation height as water and nutritious grass would be abundant throughout the study site.

2.1.4 Approach

To meet the objectives outlined above, I collected data for a suite of environmental variables (grass height, grass biomass, greenness, grass species composition, grass protein, soil N, P, K, woody cover, elevation, distance to water, and distance to human habitation) and the corresponding animal densities at representative sites across the study area. I condensed many of the related variables using principal component analysis (Hotelling 1933) to reduce multicollinearity. I built Poisson or negative binomial regression models for each species by season data set. I performed model selection and model averaging using Akaike 's Information Criterion (AIC) described by Burnham and Anderson (2002) to evaluate the models that best explained species resource selection.

2.2 Methods

2.2.1 Study design

I performed this study in a 62 km² fenced wildlife sanctuary within Gorongosa National Park in central Mozambique (18° 58‘ S, 34° 15‘ E). All large grazing herbivores - African buffalo (*Synercus caffer*), blue wildebeest (*Connochaetes taurinus*), and Burchell's zebra (*Equus burcellii*) – were nearly extirpated from the park at the end of the Mozambican civil war in 1992. Between 2006 and 2009, 85 buffalo and 180 wildebeest were reintroduced to the wildlife sanctuary in the park. At the time of this study, the sanctuary contained African buffalo, blue wildebeest, bushbuck (*Tragelaphus scriptus*), common reedbuck (*Redunca arundinum*), greater kudu (*Tragelaphus strepseceros*), common duiker (*Sylvicapra grimmia*), impala (*Aepyceros melampus*), lichtenstein’s hartebeest (*Alcelaphus lichtensteinii*), nyala (*Tragelaphus angasii*), oribi (*Ourebia ourebia*), red duiker (*Cephalophus natalensis*), sable antelope (*Hippotragus niger*), and waterbuck (*Kobus ellipsiprymnus*). Lion (*Panthera leo*), leopard (*Panthera pardus*), and other large predators were excluded from the sanctuary, as were hippopotamus (*Hippopotamus amphibius*) and elephant (*Loxodonta africana*).

I performed a 1-yr-long study (from November 2009 to November 2010) in which I collected data on animal density, vegetation properties (grass height, biomass, species, greenness, and crude protein), and soil nutrients (nitrogen, phosphorous, and potassium). I repeated sampling during three seasons: wet season (December 2009 – March 2010), early dry season (April 2010 – July 2010), and late dry season (August 2010 – November 2010). During the study period, average monthly rainfall in the wet season and early dry season was 275.7mm and 44.3mm respectively. Rainfall data for the late dry season in 2010 were not available but the average monthly rainfall for this season in 2009 was 52.2mm.

I established forty-eight 30m x 30m plots in a stratified random design (Brewer 2007) where eight plots were randomly placed within each of six strata. The strata were comprised of three vegetation types - savanna, salt plain (i.e. sodic savanna), and floodplain - crossed with unburned and burned areas (Fig 2.1). The burned area was formed by a large wildfire that burned 52% of the sanctuary in September 2009. The miombo woodland vegetation type was omitted from analysis in this study due to poor road access. The plot locations were constrained to a minimum distance of 100m between each plot and from the edge of the strata.

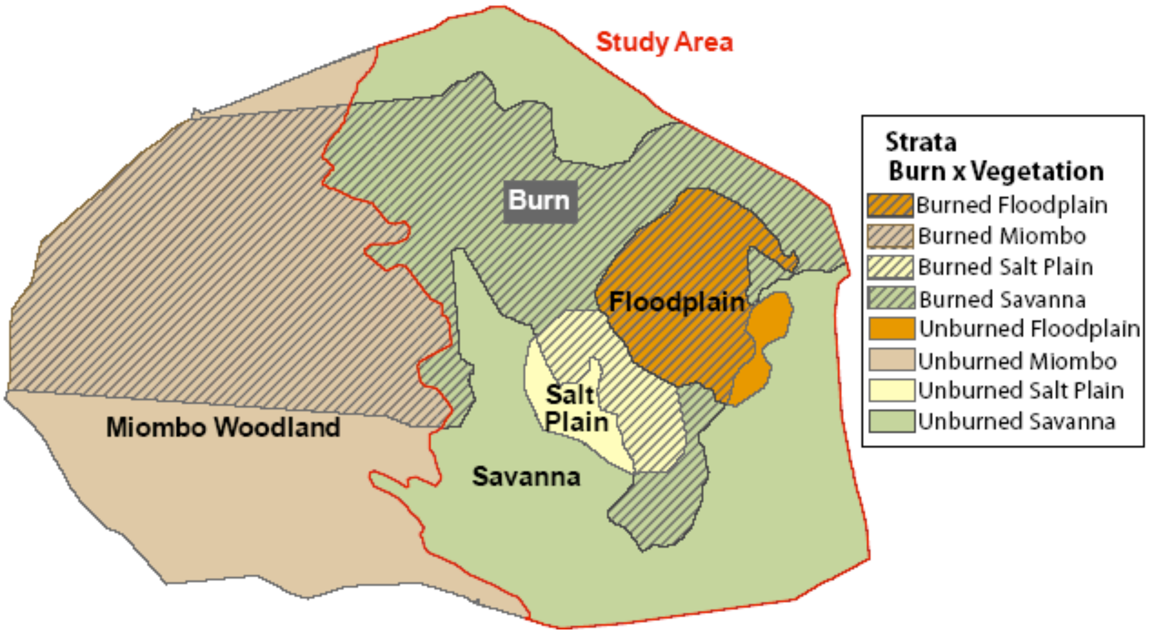


Figure 2.1 Map of the study area within the wildlife sanctuary of Gorongosa National Park. The study area (outlined in red) is comprised of six strata. Solid colors are unburned savanna (green), salt plain (yellow), and floodplain (orange). Hatched areas are burned savanna, salt plain and floodplain.

I randomly assigned a mowing treatment to half of the 30m x 30m plots within each strata and mowed these plots at the beginning of each season (December 2009, April 2010, and August 2010) after I completed dung and vegetation sampling for the previous season.

2.2.2 Data collection

I collected all dung, vegetation, and soil data at the end of each season (March 2010, July 2010, November 2010). Three 30m x 2m dung quadrats were spaced 10m apart within the 30m x 30m plots (Figure 2.2). I cleared dung from the 30m x 2m quadrats at the beginning of the project (November 2009) and resampled them at the end of each season following methods described by Krebs *et al.* (1987, 2001). Wildebeest and buffalo dung piles were counted and the dung was crushed to prevent recounting during the following season.

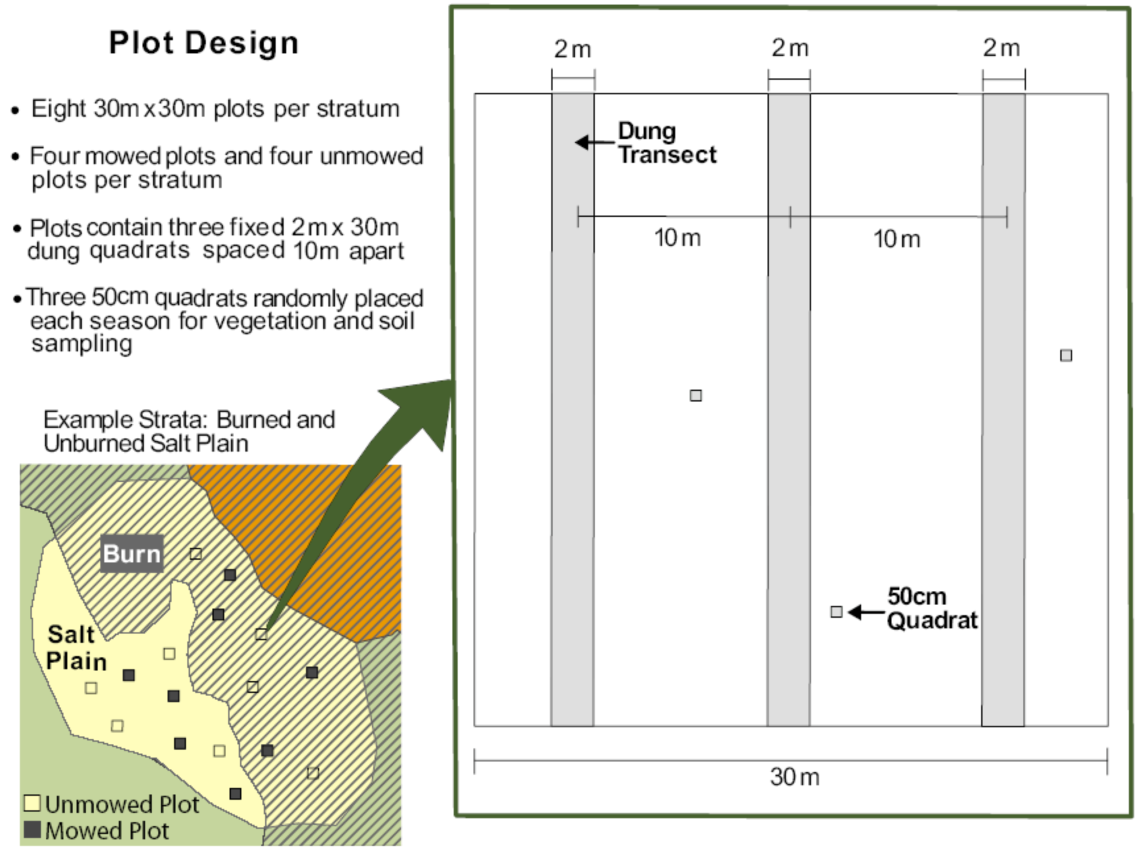


Figure 2.2 Study design depicting plots within strata and quadrats within plots.

I assessed dung decomposition to ensure that wildebeest and buffalo dung would not decompose during each season, which could result in undercounting (Laing *et al*. 2003). To do this, I collected a minimum of five fresh dung piles per species at the beginning of each season and I verified that the dung was identifiable at the end of the season.

During each sampling period, I collected vegetation data at 3 random points within the 30m x 30m plots (Figure 2.2). At each point, I measured the height of the tallest clump of grass within a 50cm square quadrat. I sampled total biomass and percent green biomass by harvesting all aboveground vegetation and leaf litter within the vertical projection of the same 50cm quadrat (Shaver *et al*. 2001). I separated the vegetation into green vegetation, brown vegetation, and leaf litter, and subsequently dried and weighed it. I sampled grass species using a 1m wide point frame with 10 pins spaced 10cm apart to measure grass species composition. I recorded the total number of times an individual of a species touched a pin (“# of hits”) (Whitman and Siggeirsson 1954).

I performed a visual estimate of percent woody cover within the 30m x 30m plots. I collected soil and grass samples for laboratory analysis of soil nitrogen (total-N), soil phosphorus (extractable P), soil potassium (extractable K), and grass protein (% crude protein).

I performed line-transect sampling (Buckland *et al.* 2001, Augustine 2010) to estimate buffalo and wildebeest densities. I used these data to determine whether dung estimates were strongly correlated with wildebeest and buffalo density estimates (Krebs *et al.* 1987, 2001). I selected eleven 1km transects in a stratified random fashion along straight sections of road through the three vegetation types (floodplain, salt plain, and savanna) within the study area. I resampled the transects monthly for 8 months (April – November 2010). Poor road access during the wet season made it impossible to perform surveys during this season. Surveys were conducted from a Land Cruiser driven at an average speed of 10km/hr with 2-4 observers and 2 data recorders seated in the back of the truck. Surveys were conducted just after sunrise and just before sunset. For each animal sighting the species, size of the herd, distance to the transect, and angle of the center of the herd to the transect was recorded.

2.2.3 Statistical analysis

Ordination

I obtained species abundance data for 12 grass species (Appendix A). The individual species data displayed unimodal species response curves on long gradients which are characterized by many zeros in the dataset. I performed transformation-based PCA (tb-PCA) using a Hellinger transformation on the log-transformed grass species abundance data which is considered suitable for species abundance data with many zeros (Legendre and Legendre 1998, Legendre and Gallagher 2001). After assessing normality and linearity of the principal components, I selected the first three principal components to represent grass species composition for the set of explanatory variables in model selection (Cleary *et al.* 2005).

I performed a second series of PCAs on seven vegetation and soil variables (total biomass, percent green biomass, height, grass protein, soil nitrogen, soil phosphorous, and soil potassium). I examined the raw univariate data for normality, log transformed the data, and removed influential outliers where necessary. I standardized each set of data to a mean of zero and standard deviation of one before performing the analysis. After assessing normality and linearity of the principal components, I selected the first principal component to represent vegetation and soil characteristics for the set of explanatory variables in model selection (Cleary *et al*. 2005).

Dung and Sighting Density Correlation

I calculated wildebeest densities monthly for each vegetation type (savanna, salt plain and floodplain) from line transect data using the software program DISTANCE 6.0 (Buckland *et al*. 2001). I then averaged the monthly density estimates for each vegetation type within the two seasons (early season and late dry season) resulting in six population density estimates. I also averaged dung densities for the two seasons within the three vegetation types. I observed buffalo too infrequently to calculate accurate densities for any season. I calculated Pearson's correlation coefficient for dung densities vs. wildebeest densities.

Model Selection - Ecological Models

I selected thirty-nine models *a priori* to determine the models that best predicted resource selection by the wildebeest and buffalo (Table 2.1). The wet and late dry season models were generalized linear models with Poisson variance functions. Data from the early dry season for both species were overdispersed, so I used negative binomial variance functions. The models fall within seven categories which have been determined to play a significant role in resource selection by large grazing herbivores (Western 1975, McNaughton 1988, Fryxell 1991). The model categories are forage quality, forage quantity, forage value (e.g. forage quality and quantity), broad-scale factors (e.g. vegetation type and burn), forage type, abiotic factors, and forage value with abiotic factors. I chose these models to determine which of the seven categories, and which variables within the selected categories, best explains resource selection by each species across the three seasons.

Table 2.1 Candidate model set within seven model categories

Forage Quality	Forage Quantity	Forage Value	Broad Scale Factors	Forage Type	Abiotic Factors	Forage Value & Abiotic Factors
N + P + K	H	V1	VT	G1	E	V1 + Wa
Pr	B	B + G + B*G	Bu	G2	Wa	V1 + Wo
G	H + B	B + Pr	VT + Bu	G3	Wo	V1 + E
N + Pr		B + Pr + B*Pr	VT*Bu	G1 + G2	Hu	V1 + Hu
				G1 + G3	Wo + Hu	B + Pr + Wa
				G2 + G3	Wo + Wa	B + Pr + Wo
				G1 + G2 + G3	Wo + E	B + Pr + Hu
					E + Wa	B + Pr + E
					Wo + E + Wa	

N = Soil Nitrogen
P = Soil Phosphorous
K = Soil Potassium
Pr = % Crude protein of grass
G = % Greenness of grass
H = Height of Grass
B = Biomass of Grass
VT = Vegetation type, a categorical variable of the three vegetation classifications: Savanna, Salt Plain, and Floodplain
Bu = Burn, a categorical variable of two burn classifications, burned or unburned
V1 = 1st principal component of the ordination of height, biomass, greenness, protein, soil nitrogen, soil phosphorous, and soil potassium
G1 = 1st principal component of the ordination of grass species abundance
G2 = 2nd principal component of the ordination of grass species abundance
G3 = 3rd principal component of the ordination of grass species abundance
E = Elevation
Wa = Distance of the plot to the nearest water point
Wo = % woody cover
Hu = Distance of the plot to the nearest human habitation

I performed model selection using the information-theoretic approach (Burnham and Anderson 2002). I ranked models according to the second order Akaike's Information Criterion (AIC_c) to correct for bias because the sample size was small (48) in relation to the number of parameters (20) (Burnham and Anderson 2002). I calculated the difference in AIC_c scores between each model and the model with the lowest score (ΔAIC_c) along with Akaike weights (ω_i) and evidence ratios for all models within 4 ΔAIC_c of the best model. I calculated relative importance values for each parameter by summing the weights of all the models that contain that parameter. I averaged all models within 4 ΔAIC_c of the best model and reported model-averaged estimates, unconditional standard errors, and 95% confidence intervals for each selected model.

Model Selection – Difference in Resource Selection

I selected two sets of two models each *a priori* to determine the difference in resource selection by wildebeest and buffalo on two spatial scales. The first set of models consisted of one model with six main effects representing patch-scale grass and soil properties and one model with the same six patch-scale main effects plus a species effect:

$$y = ß_0 + V1 + V2 + V3 + G1 + G2 + G3 + Sp + \sigma$$
$$y = ß_0 + V1 + V2 + V3 + G1 + G2 + G3 + \sigma$$

where:
$ß_0$ = Intercept
V2 = 2nd principal component of the ordination of grass and soil variables
V3 = 3rd principal component of the ordination of grass and soil variables
Sp = Categorical variable (buffalo or wildebeest) representing species effect
σ = Standard Error

I performed a separate model selection analysis on the second set of models which consisted of one model with six main effects representing landscape-scale characteristics and one model with the same six landscape-scale main effects plus a species effect:

$$y = ß_0 + VT + Bu + Wo + Wa + E + Hu + Sp + \sigma$$
$$y = ß_0 + VT + Bu + Wo + Wa + E + Hu + \sigma$$

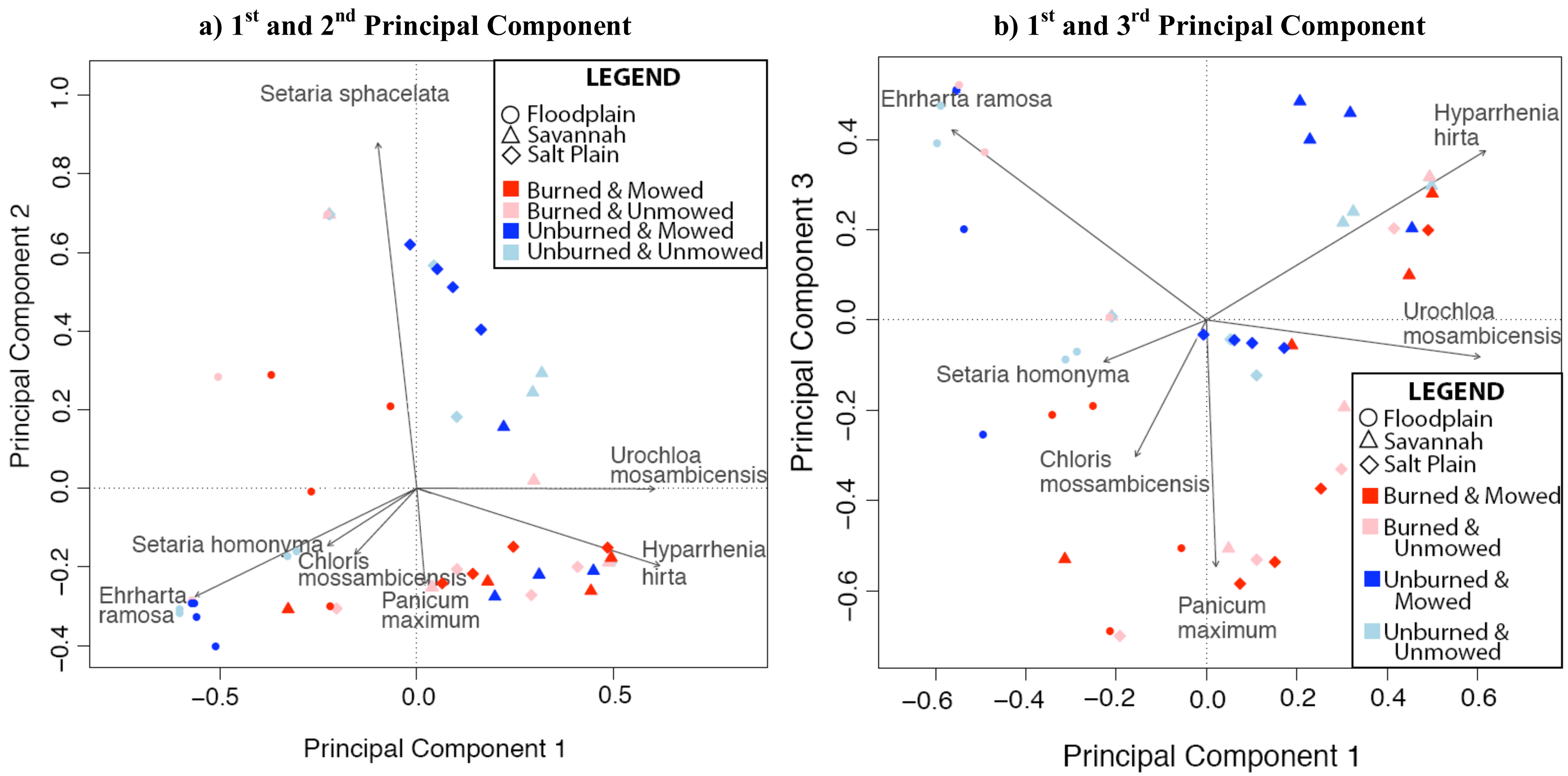
High ΔAICs in favor of the models including the species effect would indicate difference in resource selection by the two species.

2.3 Results

2.3.1 Ordination

Grass Species Composition

For each season dataset, I performed a PCA on grass species (Figures 2.3, 2.4, and 2.5) and a separate PCA on vegetation and soil properties (Figures 2.6, 2.7, 2.8, and 2.9). The results of the grass species ordination showed that grass species composition varied by vegetation type and burning in every season. For the wet season ordination, the first three principal components were used in model selection. These principal components represent 1) a continuum from floodplain [low values] to savanna and salt plain communities [high values] (Figure 2.3a); 2) a continuum from a mixture of vegetation types [low values] to unburned salt plain communities [high values] (Figure 2.3a); and 3) a continuum from burned patch communities [low values] to unburned savanna communities [high values] (Figure 2.3b).


a) 1st and 2nd Principal Component

b) 1st and 3rd Principal Component

Figure 2.3 Biplots of grass species community ordination during the wet season showing the first (x-axis) and the second (y-axis) principal components (a) and the first (x-axis) and the third (y-axis) principal components (b). Plots symbols represent vegetation types and plot colors represent burned and mowed status.

The first three early dry season principal components represent 1) a continuum from floodplain [low values] to savanna and salt plain communities [high values] (Figure 2.4a); 2) a continuum from salt plain [low values] to floodplain [near zero] to savanna communities [high values] (Figure 2.4a); and 3) a continuum from burned floodplain and salt plain [low values] to unburned floodplain communities [high values] (Figure 2.4b).

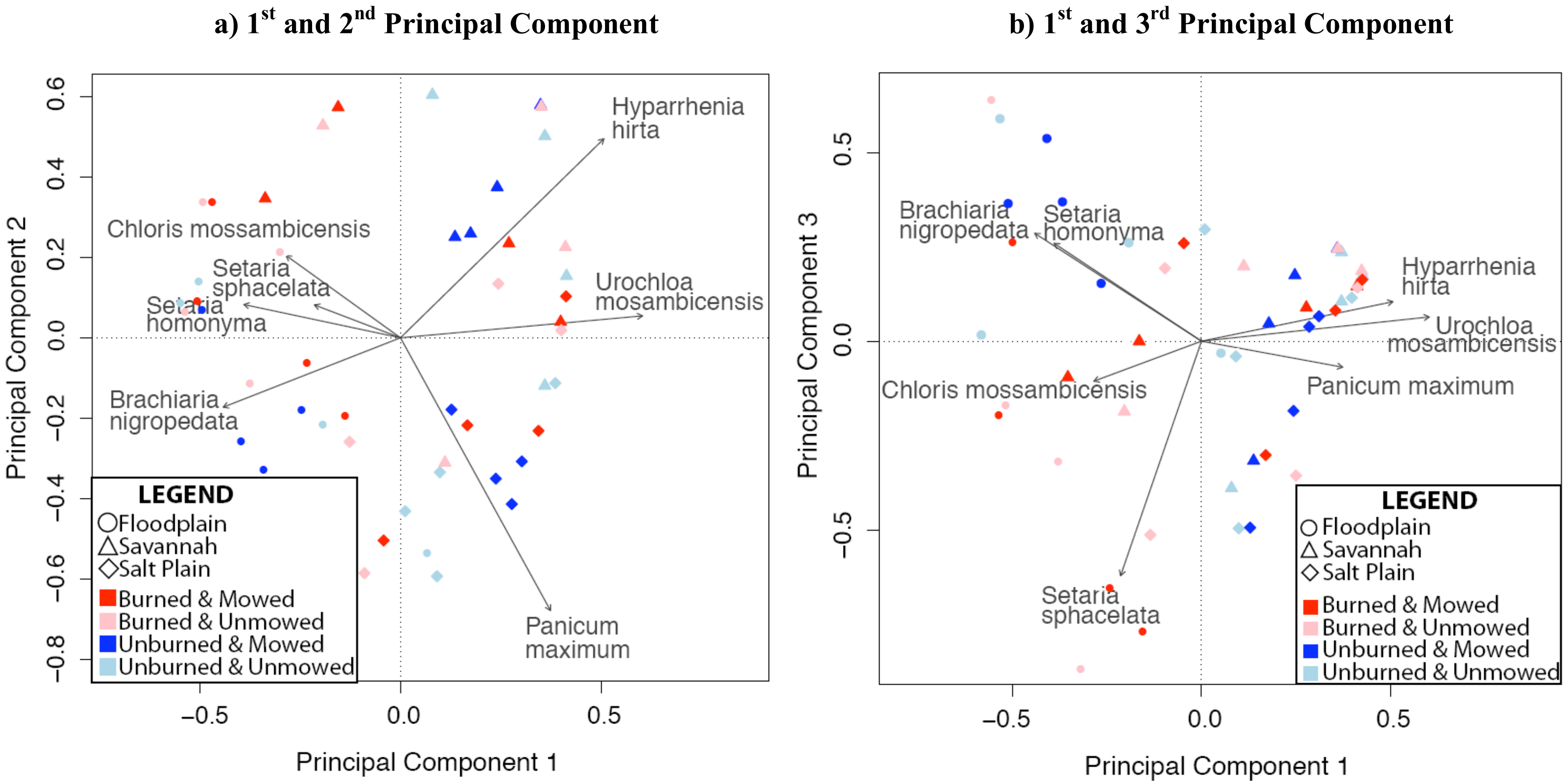
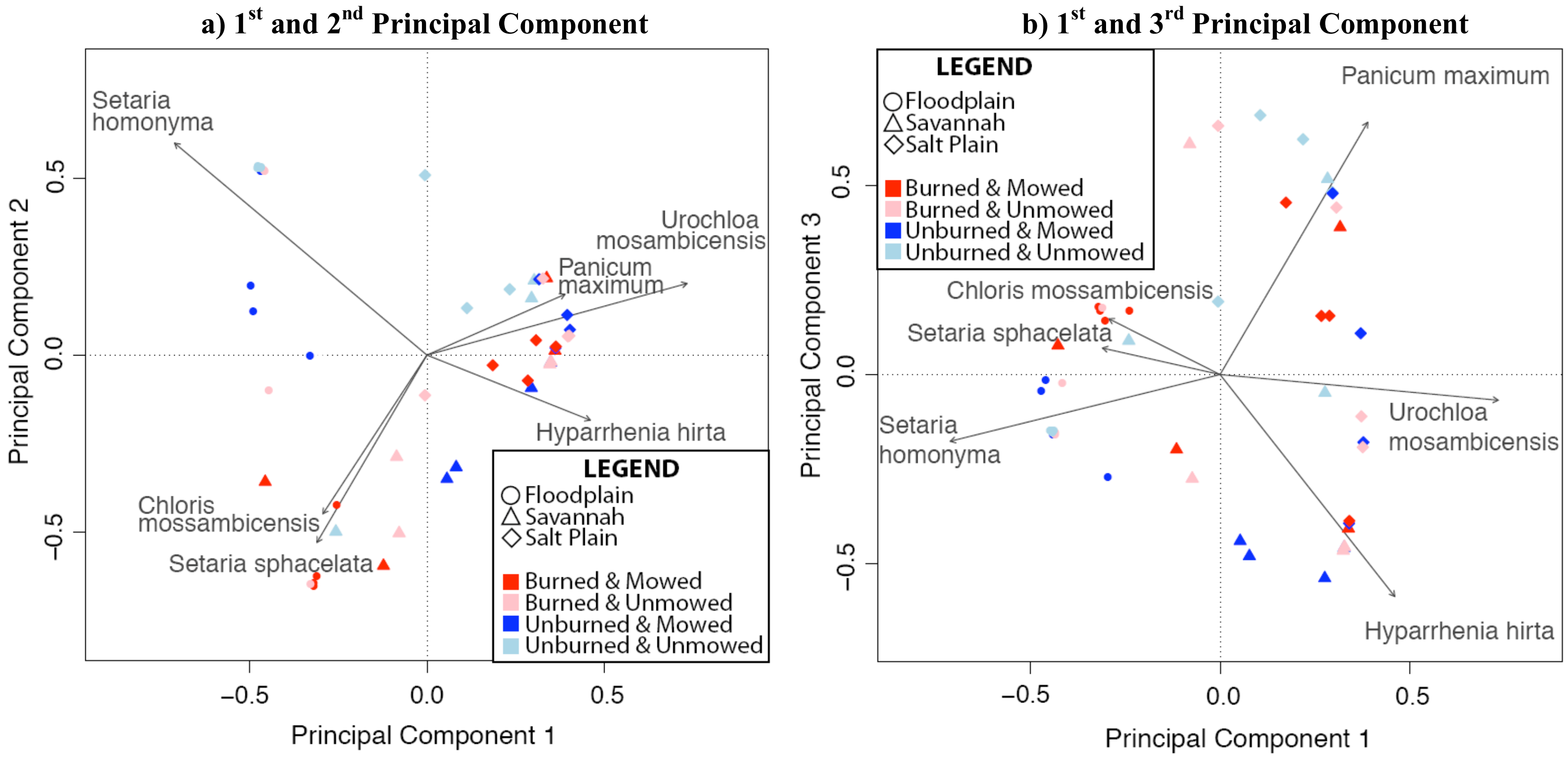


Figure 2.4 Biplots of grass species community ordination during the early dry season showing the first (x-axis) and the second (y-axis) principal components (a) and the first (x-axis) and the third (y-axis) principal components (b). Plots symbols represent vegetation types and plot colors represent burned and mowed status.

The first three late dry season principal components represent 1) a continuum from floodplain [low values] to savanna and salt plain communities [high values] (Figure 2.5a); 2) a continuum from burned floodplain and savanna [low values] to unburned floodplain and salt plain communities [high values] (Figure 2.5a); and 3) a continuum from savanna [low values] to salt plain and burned savanna communities [high values] (Figure 2.5b).


a) 1st and 2nd Principal Component

b) 1st and 3rd Principal Component

Figure 2.5 Biplots of grass species community ordination during the late dry season showing the first (x-axis) and the second (y-axis) principal components (a) and the first (x-axis) and the third (y-axis) principal components (b). Plots symbols represent vegetation types and plot colors represent burned and mowed status.

Vegetation and Soil Variables

The first principal component in the ordination of vegetation and soil variables in all three seasons represents a continuum from unmowed areas with tall grass, high grass biomass, low grass protein and low greenness [low values] to mowed areas with short grass, low biomass, and high grass protein [high values] (Figure 2.6). High greenness was associated with mowed areas in the wet season only, while soil phosphorous was associated with mowed areas in the early and late dry seasons.

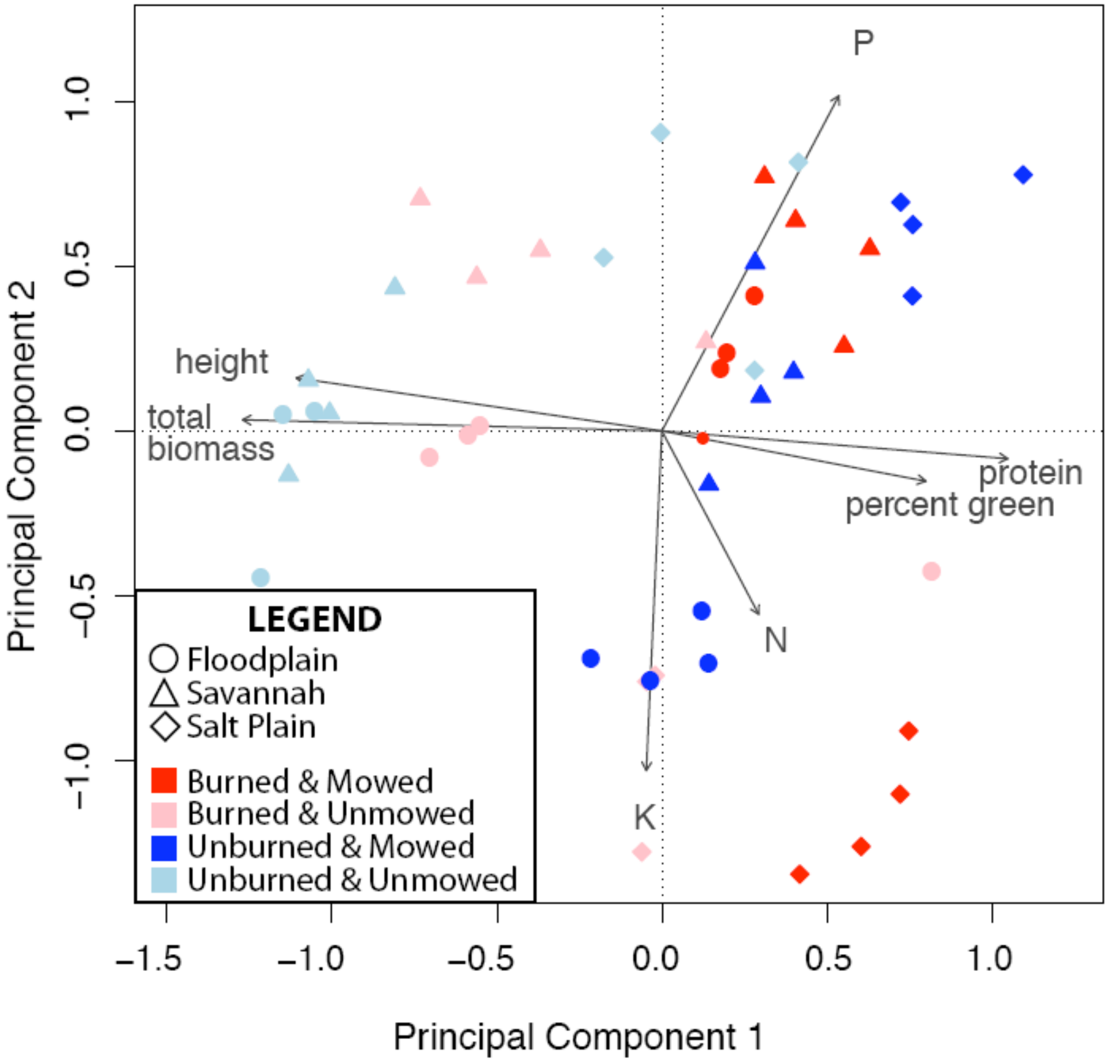


Figure 2.6 Ordination of vegetation and soil variables during the wet season showing the first (x-axis) and the second (y-axis) principal components. Plots symbols represent the vegetation types and plot colors represent burned and mowed status.

The second principal component of the wet season ordination represents a continuum from high soil nitrogen and potassium and low soil phosphorous [low values] to high soil phosphorous and low soil nitrogen and potassium [high values] (Figure 2.6). There was not a strong trend in the third principal component, but it weakly represents a continuum from high percent greenness and low soil potassium and phosphorous [low values] to high soil potassium and phosphorous and low percent greenness [high values] (Figure 2.7).

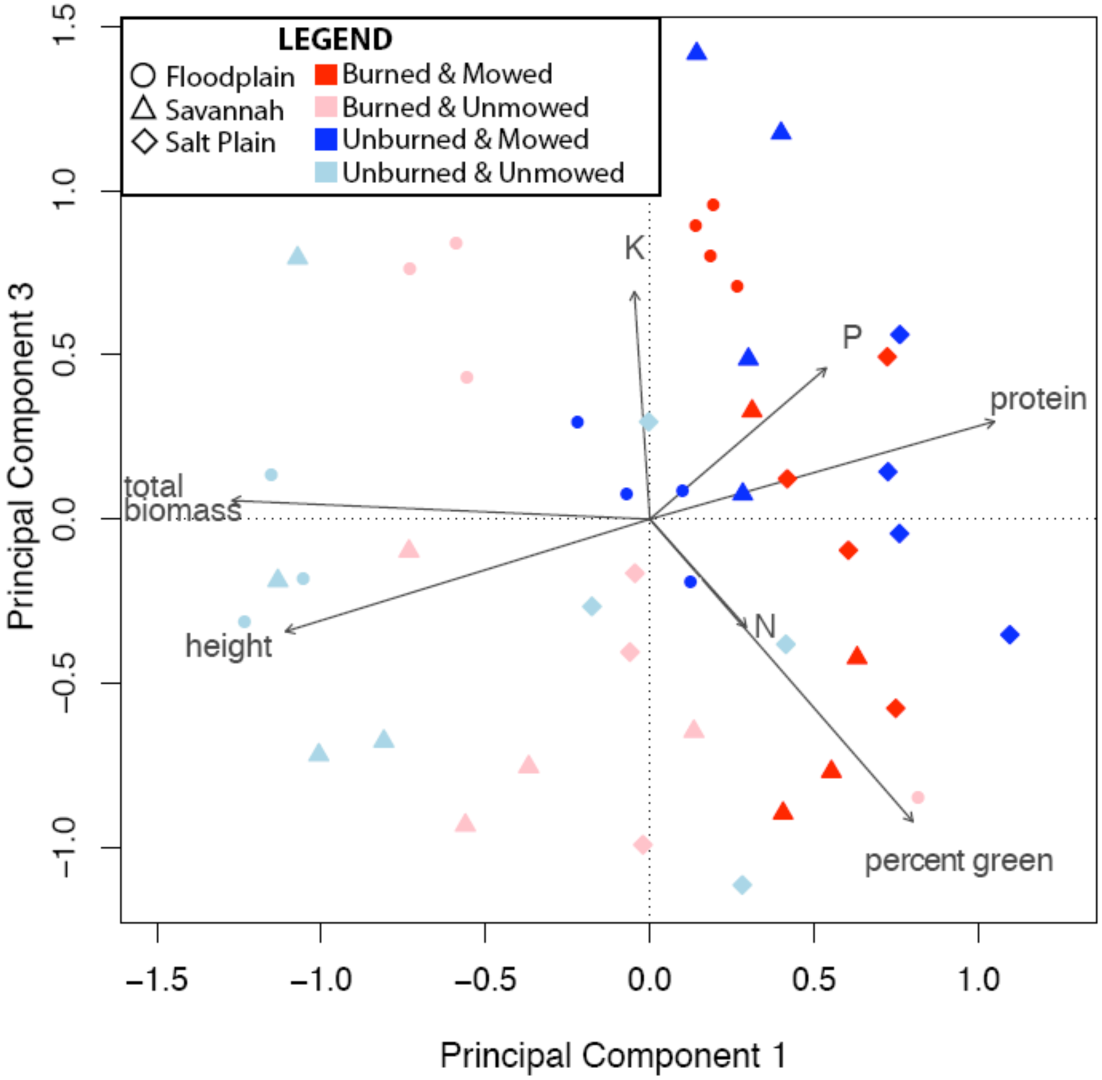


Figure 2.7 Ordination of vegetation and soil variables during the wet season showing the first (x-axis) and the third (y-axis) principal components. Plots symbols represent the vegetation types and plot colors represent burned and mowed status.

The second and third principal components of the early dry season ordination represent 1) a continuum from high soil potassium and low soil nitrogen and grass greenness [low values] to high soil nitrogen and grass greenness and low soil potassium [high values]; and 2) a continuum from high soil phosphorous and nitrogen and low soil potassium and grass greenness [low values] to high soil potassium and grass greenness and low soil phosphorous and nitrogen [high values] (Figure 2.8).

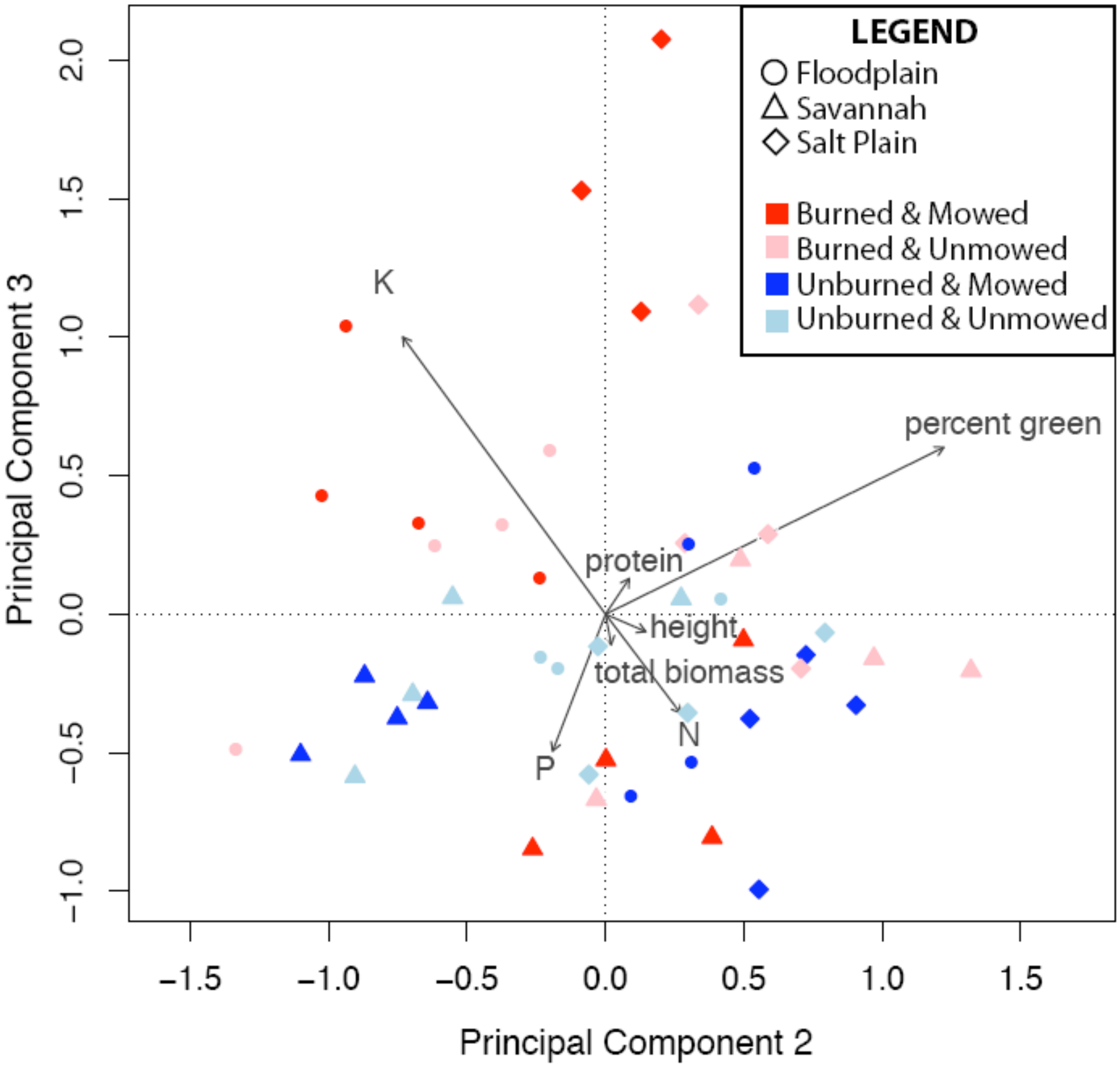


Figure 2.8 Ordination of vegetation and soil variables during the early dry season showing the second (x-axis) and the third (y-axis) principal components. Plots symbols represent the vegetation types and plot colors represent burned and mowed status.

The second and third principal components of the late dry season ordination represent 1) a continuum from high soil nitrogen and grass greenness and low soil potassium [low values] to high soil potassium and low soil nitrogen and grass greenness [high values]; and 2) a continuum from high soil phosphorous and low soil potassium [low values] to high soil potassium and low soil phosphorous [high values] (Figure 2.9).

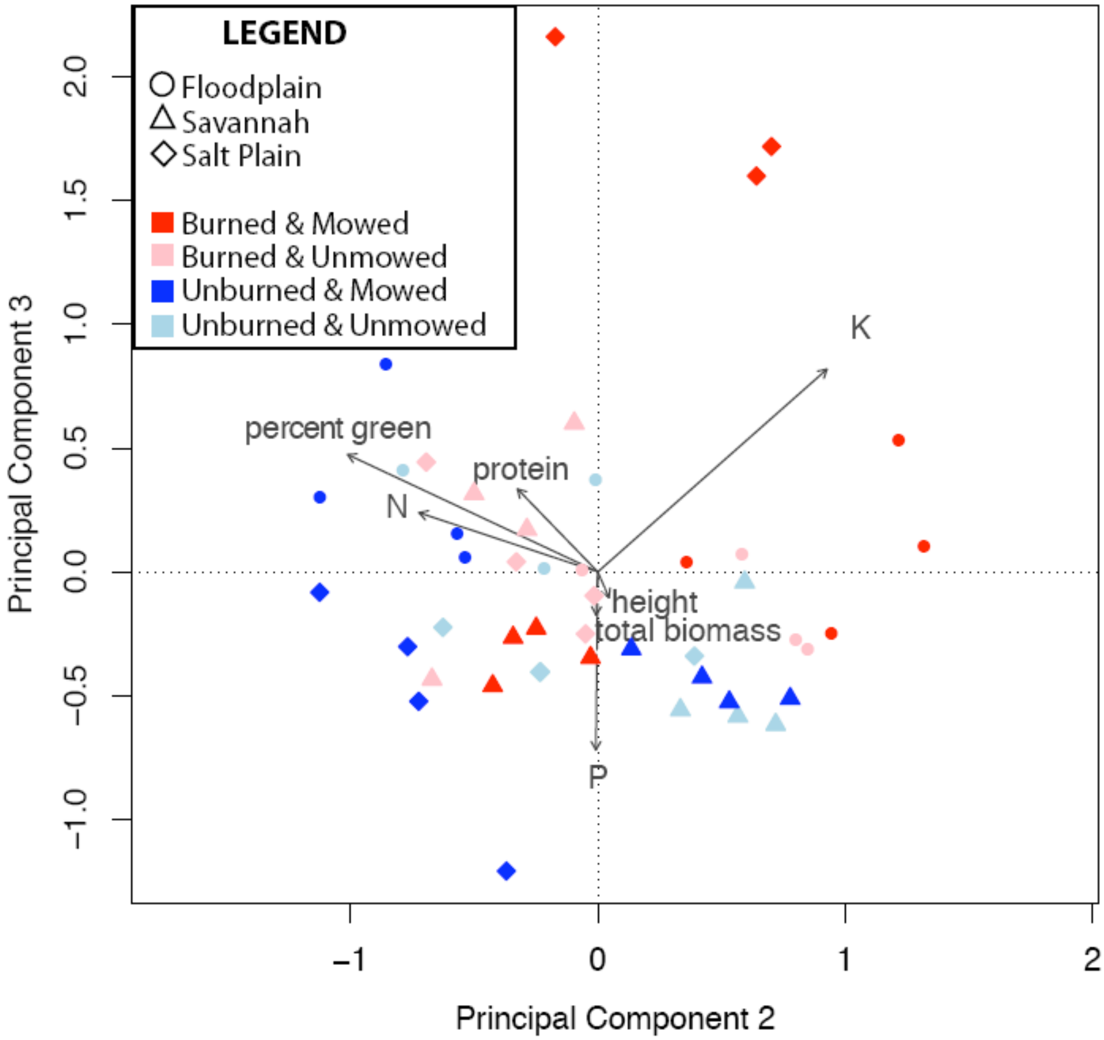


Figure 2.9 Ordination of vegetation and soil variables during the late dry season showing the second (x-axis) and the third (y-axis) principal components. Plots symbols represent the vegetation types and plot colors represent burned and mowed status.

2.3.2 Dung and sighting correlation

Dung density and animal sighting density by season and vegetation type were highly correlated for wildebeest ($R^2=0.989$). Insufficient observations of buffalo precluded a comparison for this species. Based on the high correlation of dung and sighting data for wildebeest, it was appropriate to use dung density to represent animal density for both species.

2.3.3 Model selection – ecological models

Buffalo – Wet Season

The set of candidate models (Table 2.1) were fit using wet season environmental variables as the explanatory variables and buffalo dung counts as the response variable. The global model including all explanatory variables fit the data based on a chi-square goodness of fit test (p=1). Model selection resulted in six models with $\Delta AIC_c < 4$ (Table 2.2). $\Delta AIC_c < 4$ is used as a cutoff point because models with > 4 ΔAIC_c have substantially less support than models with < 4 ΔAIC_c (Burnham and Anderson, 2002). In some cases, only the models with < 2 ΔAIC_c are considered when appropriate.

Four of the selected models were in the “forage type” category which indicates that grass species composition was an important factor in buffalo resource selection during the wet season. One model was in the “forage value and abiotic factors” category which included the first vegetation and soil principal component (V1) and woody cover (Wo). Another model was in the “forage value” category which included only the first vegetation and soil principal component (V1). These two models indicate that vegetation height and quantity, forage quality, and shade or perceived predator avoidance were important factors in buffalo resource selection during the wet season. Model averaged estimates of the variables in the selected model set were calculated with their associated standard errors and 95% confidence intervals (Table 2.3).

Table 2.2 Selected models (<4 ΔAIC_c) of buffalo resource selection.

Model Category	Model Variables	K	AIC_c	ΔAIC_c	ω_i	Cum ω_i	log(*L*)	Evidence Ratio
Wet Season								
Forage Type	G1 + G3	3	86.06	0.00	0.28	0.28	-39.75	1.00
Forage Value & Abiotic Factors	V1 + Wo	3	86.41	0.35	0.23	0.51	-39.92	1.19
Forage Type	G1 + G2 + G3	4	87.69	1.63	0.12	0.64	-39.37	2.25
Forage Type	G3	2	87.83	1.76	0.12	0.75	-41.78	2.41
Forage Value	V1	2	88.75	2.68	0.07	0.83	-42.23	3.82
Forage Type	G2 + G3	3	89.92	3.85	0.04	0.87	-41.68	6.87
Early Dry Season								
Forage Value & Abiotic Factors	V1 + E	4	156.12	0.00	0.36	0.36	-73.60	1.00
Forage Value	B + Pr + B*Pr	5	158.06	1.93	0.14	0.50	-73.31	2.63
Forage Quality	N + P + K	5	158.23	2.10	0.13	0.63	-73.40	2.86
Late Dry Season								
Broad Scale Factors	VT + Bu	4	89.83	0.00	0.50	0.50	-40.45	1.00
Broad Scale Factors	VT + Bu + VT*Bu	6	92.38	2.55	0.14	0.64	-39.17	3.58
Broad Scale Factors	VT	3	92.46	2.62	0.14	0.78	-42.95	3.72

K = number of model parameters

ΔAIC_c = difference in AICc value from the "best" model

ω_i = Akaike weight

Cum ω_i = cumulative Akaike weights

log(*L*) = log likelihood

Table 2.3 Model averaged estimates of parameters in all selected models (<4 ΔAIC_c) of buffalo resource selection.

	Estimate*	SE**	Lower CI	Upper CI***
Wet Season				
(Intercept)	-0.90	0.93	-2.72	0.92
G1	4.12	2.22	-0.22	8.47
G2	1.34	1.76	-2.12	4.79
G3	-6.14	1.74	-9.55	-2.72
V1	2.06	1.65	-1.17	5.29
Wo	-0.74	0.43	-1.58	0.10
Early Dry Season				
(Intercept)	1.50	4.55	-7.42	10.43
V1	4.05	1.42	1.28	6.83
E	-0.59	0.24	-1.06	-0.13
B	-0.12	0.33	-0.76	0.52
Pr	0.10	0.06	-0.02	0.22
B*Pr	0.21	0.07	0.07	0.36
N	2.51	4.82	-6.94	11.96
P	0.02	0.01	0.01	0.03
K	2.82	1.51	-0.14	5.77
Late Dry Season				
(Intercept)	-1.09	1.05	-3.16	0.98
VT (Salt Plain)	1.73	0.63	0.51	2.96
VT (Savanna)	0.51	0.73	-0.92	1.94
Bu (Unburned)	-0.94	0.45	-1.82	-0.07
VT(Salt Plain):Bu(Unburned)	16.72	2021.45	-3945.26	3978.69
VT(Savanna):Bu(Unburned)	15.94	2021.45	-3946.04	3977.91

* Model-averaged estimate
** Unconditional SE
*** 95 % Unconditional confidence interval

Importance values were calculated for each variable in the selected model set. The most important variable in the model set was G3 (grass species principal component 3) which had an importance value of 0.56. The model averaged estimate of G3 indicates that buffalo density was negatively associated with G3 (Table 2.3). During this season, low values of G3 represented grass species communities dominated by *Panicum maximum*, which was prevalent in burned areas of all vegetation types (Figure 2.3b).

G1 (grass species principal component 1) and V1 (vegetation and soil principal component 1) also had high importance values (0.40 and 0.39 respectively). The model averaged estimate of G1 indicates that buffalo density was positively associated with G1 (Table 2.3). During this season, high values of G1 represented grass species communities dominated by *Urochloa mosambicensis* and *Hyparrhenia hirta*, which were prevalent in savanna and salt plain vegetation types (Figure 2.3a, b). The model averaged estimate of V1 indicates that buffalo density was positively associated with V1 (Table 2.3). During this season, high values of V1 represented areas with short grass, low biomass, high grass protein and high grass greenness (Figure 2.6).

Buffalo – Early Dry Season

The set of candidate models (Table 2.1) were fit using early dry season environmental variables as explanatory variables and buffalo dung counts as the response variable. The global model including all variables fit the data based on a chi-square goodness of fit test (p=.3196). Model selection resulted in three models with $\Delta AIC_c < 4$ (Table 2.2).

The “best” model was in the “forage value & abiotic factors” category which included the first vegetation and soil principal component (V1), and elevation (E). This indicates that vegetation height and quantity, forage quality, and elevation were important factors in buffalo resource selection. Although there were three models in the selected model set, only the “best” model was examined here because of its high Akaike weight and high evidence ratio (Table 2.2) indicating that there was strong evidence that the best model was a better fit than the next best model.

The most important variables in the model set were V1 (vegetation and soil principal component 1) and elevation which both had importance values of 0.57. The model averaged estimate of V1 indicates that buffalo density was positively associated with V1 (Table 2.3). During this season, high values of V1 represented areas with short grass, low grass biomass, high grass protein and high soil phosphorous. The model averaged estimate of elevation indicates that buffalo density was negatively associated with elevation (Table 2.3). Low elevation areas in the study area were encompassed predominantly by floodplain and some savanna vegetation types.

Buffalo – Late Dry Season

The set of candidate models (Table 2.1) were fit using late dry season environmental variables as explanatory variables and buffalo dung counts as the response variable. The global model including all explanatory variables fit the data based on a chi-square goodness of fit test ($p=0.7345$). Model selection resulted in three models with $\Delta AIC_c < 4$ (Table 2.2). The three selected models were in the "broad-scale factors" category. The "best" model included vegetation type (VT) and burn type (Bu) which were important factors in buffalo resource selection during the late dry season.

Although there were three models in the selected model set, only the "best" model was examined here because of its high Akaike weight and high evidence ratio (Table 2.2) indicating that there was strong evidence that the best model was a better fit than the second best model. The most important variables in the model set were VT (vegetation type) and Bu (burn) which had importance values of 1 and 0.82 respectively. The model averaged estimates of the savanna and salt plain vegetation types indicate that buffalo density was positively associated with both vegetation types but was more strongly associated with savanna during this season (Table 2.3). The model averaged estimate of unburned areas indicates that buffalo density was negatively associated with unburned areas (Table 2.3).

Wildebeest - Wet Season

The set of candidate models (Table 2.1) were fit using wet season environmental variables as explanatory variables and wildebeest dung counts as the response variable. The global model including all explanatory variables fit the data based on a chi-square goodness of fit test (p=1). Model selection resulted in eight models with $\Delta AIC_c < 4$ (Table 2.4). Five of the top models were in the “forage value and abiotic factors” category which shows that quality and quantity of forage along with abiotic environmental factors were important in wildebeest resource selection during the wet season. Distance to water was the most important of these abiotic factors.

Two models were in the “forage value” category. Another model was in the “forage quantity” category and included only the grass biomass variable. This indicates that forage quality and quantity were important factors in wildebeest resource selection. Model averaged estimates of the variables in the selected model set were calculated with their associated standard errors and 95% confidence intervals (Table 2.5).

Table 2.4 Selected models (<4 ΔAIC_c) of wildebeest resource selection.

Model Category	Model	K	AICc	Δi	ωi	Cum ωi	log(*L*)	Evidence Ratio
Wet Season								
Forage Value & Abiotic Factors	V1 + Wo	3	86.76	0.00	0.27	0.27	-40.10	1.00
Forage Value & Abiotic Factors	B + Pr + Wo	4	87.92	1.16	0.15	0.42	-39.49	1.78
Forage Value	V1	2	88.41	1.65	0.12	0.54	-42.07	2.28
Forage Value & Abiotic Factors	V1 + Wa	3	89.08	2.32	0.08	0.63	-41.25	3.19
Forage Value & Abiotic Factors	V1 + E	3	89.91	3.15	0.06	0.68	-41.67	4.82
Forage Quantity	B	2	90.05	3.29	0.05	0.73	-42.89	5.18
Forage Value	B + Pr	3	90.49	3.73	0.04	0.78	-41.97	6.46
Forage Value & Abiotic Factors	V1 + Hu	3	90.60	3.84	0.04	0.82	-42.02	6.82
Early Dry Season								
Forage Value & Abiotic Factors	V1 + Wa	4	209.60	0.00	0.45	0.45	-100.40	1.00
Forage Value	B + G + B*G	5	211.90	2.27	0.14	0.59	-100.20	3.11
Forage Value & Abiotic Factors	B + Pr + Wa	5	211.90	2.29	0.14	0.74	-100.20	3.14
Late Dry Season								
Forage Quality	Pr	2	91.86	0.00	0.17	0.17	-43.80	1.00
Forage Value & Abiotic Factors	V1 + Wo	3	92.29	0.43	0.14	0.30	-42.87	1.24
Forage Value & Abiotic Factors	B + Pr + Wo	4	92.40	0.54	0.13	0.43	-41.74	1.31
Forage Quality	N + Pr	3	93.75	1.89	0.07	0.50	-43.60	2.58
Forage Value	B + Pr	3	93.91	2.05	0.06	0.56	-43.68	2.79
Forage Quantity	B	2	94.05	2.19	0.06	0.61	-44.89	2.99
Forage Value & Abiotic Factors	V1 + Wa	3	94.17	2.31	0.05	0.67	-43.81	3.18
Forage Value & Abiotic Factors	B + Pr + Wa	4	94.51	2.65	0.04	0.71	-42.79	3.77
Forage Quantity	H	2	94.52	2.66	0.04	0.76	-45.13	3.78
Forage Value	V1	2	94.66	2.80	0.04	0.80	-45.20	4.06
Forage Value & Abiotic Factors	B + Pr + Bo	4	94.77	2.91	0.04	0.84	-42.92	4.29
Forage Value	B + Pr + B*Pr	4	95.30	3.44	0.03	0.87	-43.18	5.58

Table 2.5 Model averaged estimates of parameters in all selected models (<4 ΔAIC_c) of wildebeest resource selection.

	Estimate*	SE**	Lower CI	Upper CI***
Wet Season				
(Intercept)	-0.51	1.97	-4.36	3.34
vegsoilpc1	4.17	1.75	0.74	7.60
woody	-0.69	0.41	-1.49	0.11
biomass	-0.66	0.36	-1.38	0.05
protein	0.13	0.09	-0.06	0.31
water	-0.27	0.24	-0.74	0.20
elevation	-0.18	0.23	-0.62	0.26
boma	-0.10	0.24	-0.57	0.38
Early Dry Season				
(Intercept)	0.40	2.21	-3.94	4.73
water	-0.49	0.19	-0.86	-0.11
vegsoilpc1	4.73	1.24	2.29	7.17
biomass	-0.03	0.71	-1.42	1.36
protein	0.09	0.06	-0.03	0.21
per.green	0.05	0.01	0.03	0.08
Biomass:per.green	-0.03	0.01	-0.06	0.00
Late Dry Season				
(Intercept)	-1.57	3.03	-7.52	4.37
protein	0.13	0.07	-0.01	0.28
biomass	-0.34	0.57	-1.46	0.77
woody	-0.63	0.36	-1.34	0.08
vegsoilpc1	4.14	1.57	1.07	7.22
water	-0.33	0.23	-0.78	0.12
N	3.37	2.81	-2.13	8.88
height	-0.55	0.43	-1.40	0.29
boma	-0.24	0.22	-0.67	0.18
biomass*protein	-0.10	0.10	-0.31	0.10

* Model-averaged estimate

** Unconditional standard error

*** 95 % Unconditional confidence interval

The most important variable in the model set was V1 (vegetation and soil principal component 1) which had an importance value of 0.70. The model averaged estimate of V1 indicates that wildebeest density was positively associated with V1 (Table 2.5). During this season, high values of V1 represented areas of short grass with high grass protein and high grass greenness (Figure 2.6).

Wo (percent woody cover), B (biomass), and Pr (grass protein) also had high importance values (0.51, 0.29 and 0.21 respectively). The model averaged estimate of Wo indicates that wildebeest density was negatively associated with percent woody cover (Table 2.5). The model averaged estimate of B indicates that wildebeest density was negatively associated with grass biomass (Table 2.5). The model averaged estimate of Pr indicates that wildebeest density was positively associated with grass protein (Table 2.5).

Wildebeest – Early Dry Season

The set of candidate models (Table 2.1) were fit using early dry season environmental variables as explanatory variables and wildebeest dung counts as the response variable. The global model including all explanatory variables fit the data based on a chi-square goodness of fit test (p=.0943). Model selection resulted in three models with $\Delta AIC_c < 4$ (Table 2.4). The "best" model was in the "forage value & abiotic factors" category which included the first vegetation and soil principal component (V1) and distance to water (Wa). This indicates that vegetation height and quantity, forage quality, and water were important factors. Although there are three models in the selected model set, only the "best" model was examined here because of high Akaike weight and high evidence ratio (Table 2.4) indicating that there was strong evidence that the best model fits the data better than the next best model.

The most important variables in the model set were Wa (distance to water), V1 (vegetation and soil principal component 1) and B (grass biomass) which had importance values of 0.81, 0.62, and 0.38 respectively. The model averaged estimate of Wa indicates that wildebeest density was negatively associated with increasing distances from water (Table 2.5).

The model averaged estimate of V1 indicates that wildebeest density was positively associated with V1 (Table 2.5). During this season, high values of V1 represented areas with short grass, low biomass, high grass protein and high soil phosphorous.

Wildebeest – Late Dry Season

The set of candidate models (Table 2.1) were fit using early dry season explanatory variables and wildebeest dung density data as the response variable. The global model including all explanatory variables fit the data based on a chi-square goodness of fit test ($p=0.9954$). Model selection resulted in twelve models with $\Delta AIC_c < 4$ (Table 2.4). Although there were twelve models in the selected model set, only the top three models were examined here because of their high cumulative Akaike weight and a high jump in evidence ratios (Table 2.4) from the third to fourth best model indicating that there was strong evidence that the three best models fit the data better than the fourth best model. The best model was in the "forage quality" category and included only the grass protein variable. The second and third models were in the "forage value and abiotic factors" category. Both models contained the woody cover variable. The second model contained V1 while the third model contained B (grass biomass) and Pr (grass protein).

The most important variables in the model set were Pr, B, Wo (percent woody cover) and VT (vegetation type) which had importance values of 0.63, 0.42, 0.31 and 0.27 respectively. The model averaged estimate of grass protein indicates that wildebeest density was positively associated with grass protein (Table 2.5). The model averaged estimate of grass biomass indicates that wildebeest density was negatively associated with grass biomass (Table 2.5). The model averaged estimate of woody cover indicates that wildebeest density was negatively associated with woody cover (Table 2.5). The model averaged estimate of V1 indicates that wildebeest density was positively associated with V1 (Table 2.5). During this season, high values of V1 represented areas with short grass, low biomass, high grass protein and high soil phosphorous.

2.3.4 Model selection – difference in resource selection

I assessed the differences in resource selection by wildebeest and buffalo on the patch scale and landscape scale by comparing two candidate models for each scale and each season. The two candidate models in each set were identical except for the inclusion of a species effect in one of the two models. There was no strong support for differences in resource selection by the two species on either scale during any of the three seasons. The two models in each set had Akaike differences (ΔAIC_c) < 3 which was not a substantial enough difference to support the hypothesis that wildebeest and buffalo exhibit strong differences in resource selection.

2.4 Discussion

In this study I show that in nearly all cases the distributions of both buffalo and wildebeest were driven by forage value in which they typically used habitat with short, nutrient rich grass relative to areas of tall, nutrient poor grass. For wildebeest, forage value was a primary factor in resource selection while for buffalo it was a secondary factor. During the late dry season, buffalo did not exhibit a relationship between forage value and resource selection. Instead, buffalo used savanna and salt plain that had been burned the previous year.

2.4.1 Buffalo

This study shows that drivers of buffalo resource selection varied considerably between seasons. This differs from wildebeest resource selection which showed very consistent trends across the seasons. Forage type (i.e. grass community) drove buffalo resource selection during the wet season while forage value was an important secondary factor. Forage value and abiotic factors (namely, low elevation) defined buffalo resource selection during the early dry season. Buffalo used burned salt plain and savanna habitats during the late dry season.

This variability in resource selection drivers between seasons could have been influenced by extreme seasonal weather changes in this region which can affect grass growth rates, seasonal access to low elevation areas, and grass community distribution, among other factors. The impact of fire on the landscape also changes with time since the burn. Early grass regrowth after the burn is preferred forage for some species because the young shoots are extremely high in protein and phosphorous (Whelan 1995) but the grass may be too short for some herbivores. Other species utilize post-fire grass regrowth much later as grass has grown to preferred height and still has high protein and phosphorous content (Goldammer and deRonde 2004).

Despite the variability in the factors that affected buffalo resource selection, there were some notable consistencies across the seasons. Forage value, which represents areas of short grass, low biomass, and high grass quality, was important during both wet and early dry seasons. Buffalo select vegetation to maximize nutrient intake, specifically protein, (Sinclair 1977, Prins and Beekman 2008) and clipping increases grass nutrient uptake and greenness (Ruess 1984). Buffalo feed on taller grass than many other ungulate species and buffalo select grass between 5cm – 80cm (Grunow, 1980). During the wet season, grass grew quickly and four months after the plots were mowed, the average grass height in mowed plots was 48.05cm. This is within the range of grass height that buffalo prefer. During the late dry season, grass growth was slow and the mean grass height in mowed areas at the end of this season was 18cm in contrast with the tall grass of unmowed areas which averaged 97.2cm in height. Percent grass greenness was higher in unmowed plots (18.15%) vs. mowed plots (15.62%) during this season. The higher forage quality of unmowed plots runs contrary to the assumption that clipped grass is higher in forage quality. This may explain why forage value, as defined by short grass height coupled with high grass quality, was not an important factor for buffalo during the late dry season.

Another consistency across seasons was that buffalo used the burned areas and salt plain areas during the wet and late dry seasons. During the wet season, salt plain areas were dominated by *Urochloa mosambicensis* and *Hyparrhenia hirta* and burned areas were dominated by *Panicum maximum* grass species. The grass species communities of these areas during the wet season were the underlying drivers of buffalo resource selection. Studies show that buffalo select areas of post-burn regrowth as well as areas of preferred grass species communities (Sinclair 1977). Buffalo populations in other parts of Africa prefer *Panicum maximum* and *Urochloa mosambicensis* (Macandza *et al*. 2004). Salt plain habitats (i.e. sodic savanna) are desirable for some large grazing herbivores (Levick and Rogers 2008, Scogings *et al*. 2011) due to high foliar nitrogen, phosphorous and sodium (Grant and Scholes 2006).

There were some major differences in buffalo resource selection across seasons. Low elevation was important during the early dry season which is unique to this season. Areas of low elevation were largely represented by floodplain and some savanna areas. Buffalo of the Zambezi delta in Mozambique have historically flourished in the floodplain grasslands of the delta (Beilfuss and Davies 1999). Although this may be desirable habitat, it is likely that buffalo avoid the floodplain area during the wet season due to flooding.

Buffalo resource selection in the late dry season was best explained by the broad scale variables of vegetation type and burn type. Broad scale patterns in habitat choice indicate that animals are choosing areas based on broad landscape patterns as opposed to fine scale patterns such as changes in grass species composition or plant nutrients. (Morris 1987). Buffalo resource selection was strongly associated with salt plain and weakly, but positively, associated with savanna. The underlying reasons for buffalo preference for salt plain areas cannot be verified without further investigation, however, I would speculate that proximity to water and high percent greenness of grass of these areas could be important contributing factors. Buffalo resource selection was also associated with burned areas. The burn occurred 10 months prior to the start of this season, so the preference for burned areas was related to long term effects of burning, such as grass nutrients or grass species composition. Soil nitrogen is known to increase between six months to one year after a burn (Wan *et al*. 2001). Nitrogen intake by buffalo via grass consumption is an important resource for buffalo which becomes especially critical during the late dry season (Sinclair 1977, Prins and Beekman 2008). Significant increases in crude protein can be found in plants as much as two years following an intense fire (Dewitt and Derby, 1955). Grass height is not significantly different in burned and unburned areas during this season, so this would not be a factor in buffalo preference for burned areas.

2.4.2 Wildebeest

Factors influencing wildebeest resource selection were similar across all three seasons, the most important of which was forage value (i.e. forage quality and quantity). Wildebeest preferred areas of short grass, low biomass, high protein, and high grass quality. This finding is consistent with previous studies on wildebeest resource selection which show that wildebeest prefer to graze on short grass lawns of high quality forage (Estes 1969, Wilmshurst *et al.* 1999). The dominance of tall grasses in Gorongosa suggests that there is an insufficient density of tall grass grazers (i.e. buffalo and zebra) to begin the well documented grazing succession (Vesey-Fitzgerald 1960, Bell 1971) that initiates the formation of grazing lawns. Grazing lawns are a preferred resource for wildebeest which follow buffalo and zebra in the grazing succession and can maintain these short lawns when present in sufficient densities. Higher numbers of buffalo, zebra, and wildebeest are necessary in Gorongosa to naturally establish and maintain grazing lawns. It would be prudent for conservation efforts to focus on the relocation of buffalo and zebra first, to reduce grass height, followed by wildebeest to maintain grass patches in this short grass state.

Abiotic factors were also important during all three seasons. During the wet and late dry seasons, wildebeest used open areas with low percent woody cover. Studies suggest that wildebeest prefer open areas with low woody cover for greater predator visibility (Smuts 1978). Although predators were excluded from this study site, wildebeest may be exhibiting avoidance of perceived predators. In the early dry season, wildebeest used areas that were close to water. Wildebeest (like many African ungulates) are highly dependent upon water during the dry seasons (Gaylard *et al.* 2003). It is unclear why distance to water was not an important factor during the late dry season as I had predicted.

2.4.3 Difference in resource selection

This study shows that wildebeest and buffalo resource selection was similar during all three seasons. This does not necessarily mean that there was overlap between the resource selection of the two species in time and space, it simply means that they used similar resources based on their requirements during a given season. Studies have shown that similarity in resource selection can occur for two species when both species require similar resources and there is an abundance of the required resources relative to the density of animals. This condition means that there may be low competition between the species due to availability of resources (Colwell and Futuyma 1971, Sale 1974). In cases where there are major differences in resource selection, the resource requirements of the two species may be different or there may be resource partitioning due to high animal density in relation to resource availability (Putman 1996)

2.5 Conclusion

This study identified several patterns in buffalo and wildebeest resource selection across seasons. While there were some differences in resource requirements between species and across seasons, it is clear that forage value (high grass nutrients and low biomass) was important for both species during all seasons with the notable exception of buffalo during the late dry season. In Gorongosa, grass biomass is extremely high due to the extirpation of large grazing herbivores, therefore, forage quality could be a limiting factor for these reintroduced herbivores unless sufficient areas are maintained in a short grass state by fire and/or grazing. However, during the late dry season, areas where grass has been shortened may not regrow fast enough to reach a desirable height for buffalo. It is important that overgrazing does not occur as buffalo require some areas of medium to long grass to sustain them through the dry season. Certain vegetation types and burned areas were important for buffalo in the late dry season. Areas that were burned the previous year can provide areas of high quality grass of sufficient height during the late dry season. This study also found that buffalo selected areas based on preferred grass species during the wet season. Also, abiotic factors, most notably elevation, percent woody cover and distance to water, were important depending on species and season.

The findings of this study are important to better understand the resource requirements of reintroduced ungulates in an ecosystem of extremely high grass biomass and high productivity where competition and predation are low or absent. This study is also important for the conservation of this area and for similar areas where large grazing herbivores are being reintroduced. Suitable habitat for these species can be identified and protected and habitat management can be tailored to fit the needs of these species.

This study is a baseline for further studies in Gorongosa National Park that examine resource availability, resource limits on population growth, and impacts of herbivory on resources. Further studies could also compare areas of high herbivore or predator densities to better understand the effects of competition and predation on resource selection by buffalo and wildebeest.

3 Wildebeest as patch-selective grazers and African buffalo as generalists: a study of herbivores reintroduced to a post-war landscape

3.1 Introduction

3.1.1 Reintroductions to an altered landscape

Loss of large grazing herbivores through local extirpations can significantly change the state of a landscape (Sinclair 1979, Dublin 1995, Knapp *et al*. 1999). An example of this type of change is the transition of short, productive grasslands to tall, rank grasses in the absence of large grazers. Low grazing pressure allows tall grass species and woody vegetation to outcompete short grass species that can lead to the persistence of a tall grass state or encroachment by woody vegetation (Vesey-Fitzgerald 1974, Wilmhurst *et al*. 2000). In a tall grass state, grass height can only be reduced by herbivory, natural disturbance (e.g. fire), or human modification (e.g. mowing). Mowing has successfully been used in studies to initiate grazing lawns in systems where low densities of herbivores are incapable of shifting grass patches to a short grass state (Knapp *et al*. 1999, Cromsigt and Olff 2008).

Interactions between soil, plants and wildlife in grazing lawns have been studied extensively in African landscapes (Vesey-Fitzgerald 1974, McNaughton 1984, Verweij *et al*. 2006, Archibald 2008, Cromsigt and Olff 2008). High concentrations of large grazers, such as buffalo, zebra, and wildebeest, can produce and maintain natural grazing lawns which are characterized by soils high in nitrogen, phosphorous and carbon (Ruess and McNaughton 1987), productive short grass, and grass species adapted to heavy grazing (McNaughton 1979a). Grazing lawns attract and support high herbivore densities which, in turn, input high nutrient loads into the soil via defecation (Hobbs 1996). This contributes to nitrogen and phosphorous content in soil that increases grass productivity and grass nutrients (Ruess 1984, Ruess and McNaughton 1987, Hobbs 1996). Both soil nutrients and clipping of grass stalks increases grass protein (i.e. nitrogen) (Coppock *et* *al*. 1983, McNaughton 1984, Ruess 1984) and greenness (Ruess 1984) that are indicators of highly nutritious grass. In the short term, grazing shortens grass height and in the long term, sustained grazing increases the grass height to biomass ratio as short, productive grass grows in thick mats close to the soil surface (Stobbs 1973b, McNaughton 1984). Grass communities can change over long periods of heavy grazing from dominance by thick-stalked, tall grasses to dominance by short-stemmed leafy species adapted to retain sufficient leaf area under grazing (McNaughton 1978, 1979a). Studies have explored how modifying plant height by mowing alone affects nutrients (Ruess 1984), structure (Stobbs 1973a), species composition (McNaughton 1978, 1979a, Turkington *et al*. 1993) and animal use (Moe and Wegge 1997, Archibald *et al*. 2005).

An important limiting resource for herbivores is grass protein (i.e. nitrogen) (Sinclair 1977, White 1978, Mattson 1980, Prins 1996) and herbivores may utilize high-protein grazing lawns to meet their nutrient requirements (Fryxell 1991, Augustine *et al*. 2003). Moderate levels of grazing increase compensatory growth of grass which, in turn, increases grass protein and greenness (McNaughton 1979a, b, Trlica and Rittenhouse 1993, Hobbs 1996). Both buffalo and wildebeest select highly nutritious grass, sometimes traveling long distances to find nutritious fodder during the dry season when resources are scarce (Maddock 1979, Pennycuick 1979, Murray 1995). Wildebeest are strongly driven by grass nutrient content which is exemplified by the Serengeti wildebeest migration in search of green flush during dry seasons (McNaughton 1979a, Maddock 1979, Murray 1995). Patterns of buffalo movement show that they may remain in an area for several days but can move long distances within a day to track phenology (Sinclair 1977). Buffalo are also protein-limited and exhibit bulk feeding during the dry season when they have shorter feeding times and high rumination time to digest low quality forage (Sinclair 1974, Prins, 1996).

Both species have morphological adaptations that allow them to utilize vegetation resources differently. Wildebeest have wide muzzles and teeth adapted for unselective grazing on very short grass (Bell 1971, Estes 1991). Wildebeest prefer grass less than 5cm tall but will graze on patches up to 20cm (Arsenault and Owen-Smith 2008). Buffalo have wide muzzles that allow them to graze on short grass as well as large premolars and prehensile tongues used to grab and chew clumps of tall, coarse grass (Estes 1991, Macandza *et al*. 2004, Codron 2008). Buffalo generally feed on grass between 5cm and 80cm tall (Grunow 1980) but cannot graze very short grass (<5cm) due to their mouth morphology (Estes 1991). Wildebeest and buffalo are both ruminants, allowing them to digest and extract nutrients from fibrous, low quality grass (Bell 1971, Prins and Beekman 1987, Beekman and Prins 1989)

3.1.2 Problem statement

Gorongosa National Park in Mozambique once supported high densities of large grazing herbivores with its rich landscape of short, productive grasslands (Tinley 1977). During two decades of war, three of the large grazing herbivores (buffalo, wildebeest, zebra) were nearly extirpated from the park (Anderson *et al*. 2006). Over the course of this 20-year period, the vegetation of the park shifted from a short, productive grass state (Tinley 1977) to a state of rank, overgrown grasses and forbs (*pers. obs.*). A large-scale reintroduction program is underway to restore large herbivore populations and subsequently maintain grass overgrowth (Anderson *et al*. 2006). Despite these early reintroduction efforts, the present density of herbivores remains too low to significantly alter the grass state by grazing alone.

It is important to understand how grass mowing, both as a method of initiating grazing lawns and as a proxy for future grazing lawns, affects patch use by large grazers. This will allow for better understanding of how increasing herbivore densities over time will change the landscape and how these changes will affect resource selection by herbivores. It is also important to understand how these patch level changes affect resource selection in the context of a heterogeneous landscape with varying vegetation types and burning regimes. This study serves as a foundation for future studies to address whether increasing herbivore densities can maintain an alternative stable state of short, productive grass when the state is initiated by mowing or burning.

3.1.3 Objectives and predictions

The broad objective of this study was to determine if short grass patches were a strong driver in patch selection by buffalo and wildebeest in a heterogeneous landscape. The objectives of this study were threefold: (1) to determine if grass mowing significantly affected wildebeest and buffalo patch selection across time in the context of varying vegetation types and burning regimes; (2) to examine the effects of important landscape-scale factors on wildebeest and buffalo patch selection; (3) to assess how mowing affected soil nutrients, grass nutrients, grass quantity and grass species composition. Answering these questions is important to understanding the mechanisms that underlie patch choice, the establishment of grazing lawns, and how alternative states may be initiated.

In this study I predicted that mowing would positively affect wildebeest patch use and negatively affect buffalo patch use across the landscape. I predicted that landscape-scale variables would not be significantly different in mowed and unmowed patches, therefore these variables would not significantly affect patch choice. I predicted that mowing would lower grass quantity and increase grass protein and greenness; mowing would affect soil nutrients slowly as the seasons progress; and mowing would not impact grass species composition within this one year study period.

3.1.4 Approach

I assessed whether there were significant differences between animal counts in mowed vs. unmowed areas for each of the three seasons by performing statistical comparisons between the treatment levels. I performed these analyses with and without the selected landscape-scale covariates to determine whether the covariates played an important role in patch use by buffalo and wildebeest. I then assessed differences in grass and soil properties in response to mowing.

3.2 Methods

3.2.1 Study design

I performed this study in a 62 km² fenced wildlife sanctuary within Gorongosa National Park in central Mozambique (18° 58‘ S, 34° 15‘ E). All large grazing herbivores - African buffalo (*Synercus caffer*), blue wildebeest (*Connochaetes taurinus*), and Burchell's zebra (*Equus burcellii*) – were nearly extirpated from the park by the end of the Mozambican civil war in 1992. Between 2006 and 2009, 85 buffalo and 180 wildebeest were reintroduced to the wildlife sanctuary in the park. At the time of this study, the sanctuary contained African buffalo, blue wildebeest, bushbuck (*Tragelaphus scriptus*), common reedbuck (*Redunca arundinum*), greater kudu (*Tragelaphus strepseceros*), common duiker (*Sylvicapra grimmia*), impala (*Aepyceros melampus*), Lichtenstein’s hartebeest (*Alcelaphus lichtensteinii*), nyala (*Tragelaphus angasii*), oribi (*Ourebia ourebia*), red duiker (*Cephalophus natalensis*), sable antelope (*Hippotragus niger*), and waterbuck (*Kobus ellipsiprymnus*). Lion (*Panthera leo*), leopard (*Panthera pardus*), and other large predators were excluded from the sanctuary, as were hippopotamus (*Hippopotamus amphibius*) and elephant (*Loxodonta africana*).

I performed a 1-yr-long study (from November 2009 to November 2010) in which I collected data on animal density, vegetation properties (grass height, biomass, species, greenness, and crude protein), and soil nutrients (nitrogen, phosphorous, and potassium). I repeated sampling during three seasons: wet season (December 2009 – March 2010), early dry season (April 2010 – July 2010), and late dry season (August 2010 – November 2010). During the study period, average monthly rainfall in the wet season and early dry season was 275.7mm and 44.3mm respectively. Rainfall data for the late dry season in 2010 were not available but the average monthly rainfall for this season in 2009 was 52.2mm.

I established forty-eight 30m x 30m plots in a randomized complete block design where eight plots were randomly placed within each of six blocks. The blocks were comprised of three vegetation types - savanna, salt plain (i.e. sodic savanna), and floodplain - crossed with unburned and burned areas (Fig 2.1). The burned area was formed by a large wildfire that burned 52% of the sanctuary in September 2009. The miombo woodland vegetation type was omitted from analysis in this study due to poor road access. The plot locations were constrained to a minimum distance of 100m between each plot and from the edge of the blocks.

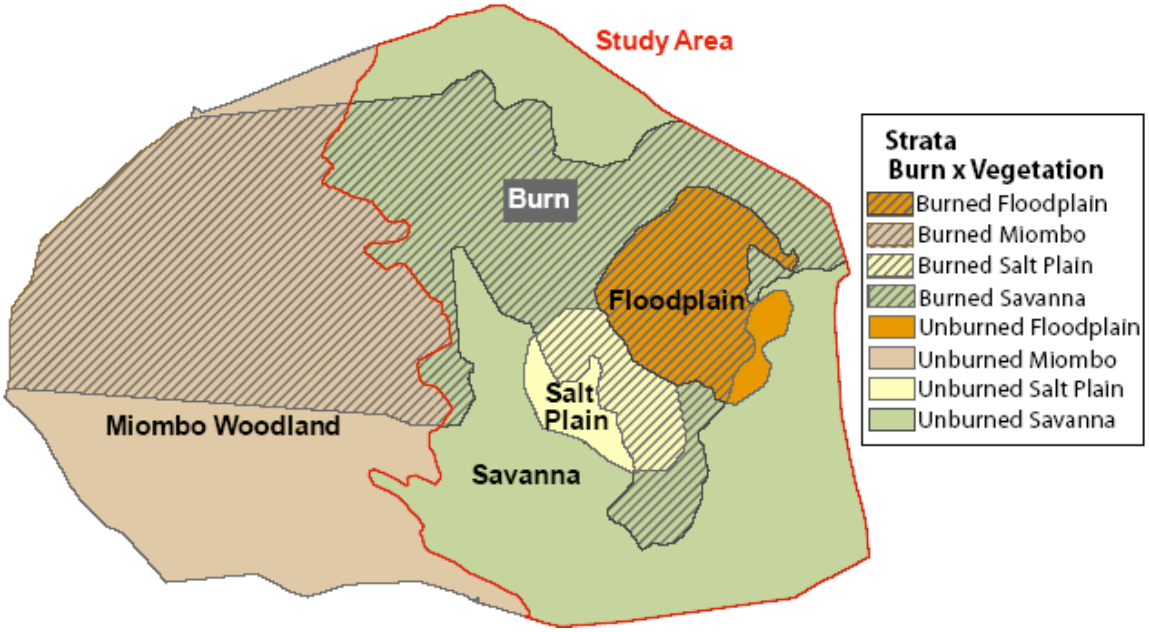


Figure 3.1 Map of the study area within the wildlife sanctuary of Gorongosa National Park. The study area (outlined in red) is comprised of six blocks. Solid colors are unburned savanna (green), salt plain (yellow), and floodplain (orange). Hatched areas are burned savanna, salt plain and floodplain.

I randomly assigned a mowing treatment to half of the 30m x 30m plots within each strata and mowed these plots at the beginning of each season (December 2009, April 2010, and August 2010) after I completed dung and vegetation sampling for the previous season.

3.2.2 Data collection

I collected all dung, vegetation, and soil data at the end of each season (March 2010, July 2010, and November 2010). Three 30m x 2m dung quadrats were spaced 10m apart within the 30m x 30m plots (Figure 3.2). I cleared dung from the 30m x 2m quadrats the beginning of the project (November 2009) and resampled them at the end of each season following methods described by Krebs *et al.* (1987, 2001). Wildebeest and buffalo dung piles were counted and the dung was crushed to prevent recounting during the following season.

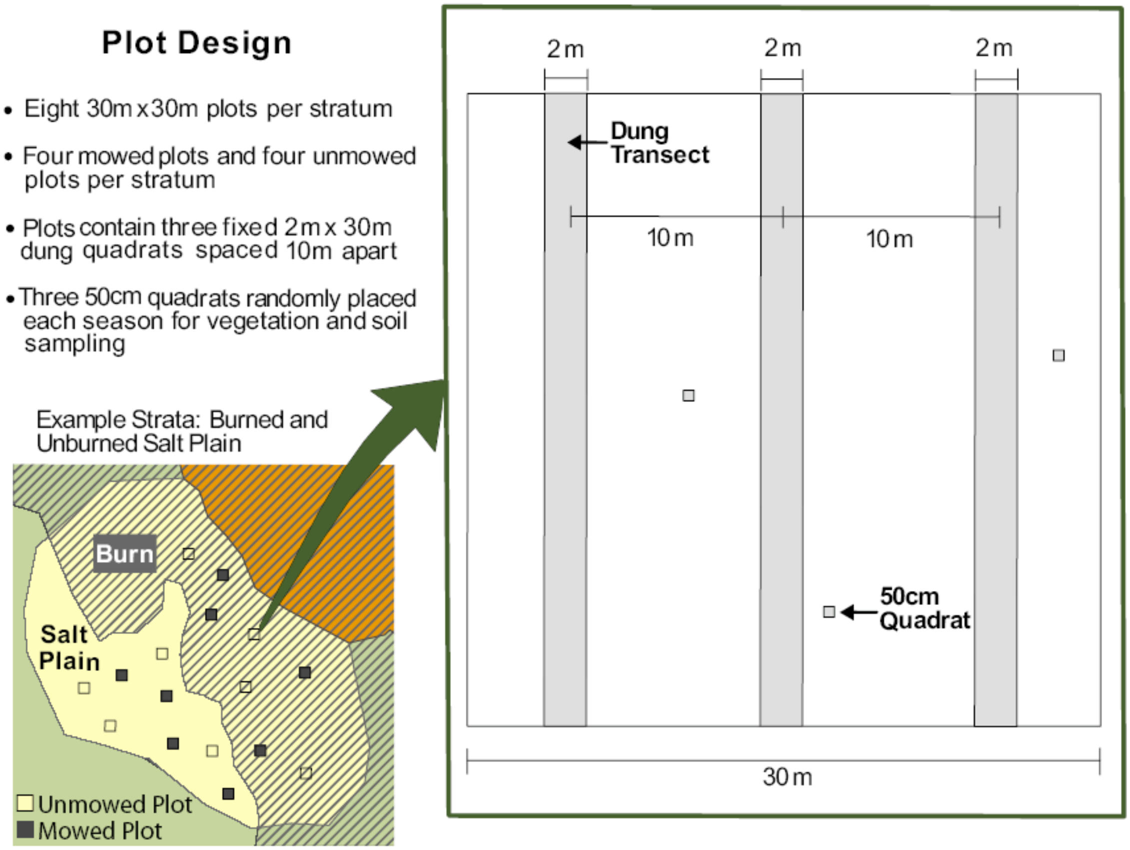


Figure 3.2 Study design depicting plots within strata and quadrats within plots.

I assessed dung decomposition to ensure that wildebeest and buffalo dung would not decompose during each season, which could result in undercounting (Laing *et al*. 2003). To do this, I collected a minimum of five fresh dung piles per species at the beginning of each season and I verified that the dung was identifiable at the end of the season.

During each sampling period, I collected vegetation data at 3 random points within the 30m x 30m plots (Figure 3.2). At each point, I measured the height of the tallest clump of grass within a 50cm square quadrat. I sampled total biomass and percent green biomass by harvesting all aboveground vegetation and leaf litter within the vertical projection of the same 50cm quadrat (Shaver *et al*. 2001). I separated the vegetation into green vegetation, brown vegetation, and leaf litter, and subsequently dried and weighed it. I sampled grass species using a 1m wide point frame with 10 pins spaced 10cm apart to measure grass species composition. I recorded the total number of times an individual of a species touched a pin ("# of hits") (Whitman and Siggeirsson 1954).

I performed a visual estimate of percent woody cover within the 30m x 30m plots. I collected soil and grass samples for laboratory analysis of soil nitrogen (total-N), soil phosphorus (extractable P), soil potassium (extractable K), and grass protein (% crude protein).

3.2.3 Statistical analysis

Ordination

I collected species abundance data for 12 grass species (Appendix A). The individual species data displayed unimodal species response curves on long gradients which are characterized by many zeros in the dataset. I performed transformation-based PCA (tb-PCA) using a Hellinger transformation on the log-transformed grass species abundance data which is considered suitable for species abundance data with many zeros (Legendre and Legendre 1998, Legendre and Gallagher 2001). After assessing normality and linearity of the principal components, I selected the first three principal components to represent grass species composition for the plots.

Environmental Response to Treatment

I performed Student's two sample t-tests to compare the means of the following variables between mowing treatments: distance to water, distance to human habitation, elevation, woody cover, grass height, grass biomass, grass protein, grass greenness, grass species composition (first three principal components), soil nitrogen, soil potassium, and soil phosphorous. Differences in selected variables across mowing treatments, burns and vegetation types over the three seasons were depicted graphically.

Herbivore Response to Treatment

I modeled the response of wildebeest and buffalo counts to the mowing treatment in three seasons using generalized linear mixed models (GLMMs) (Breslow and Clayton 1993, Bolker *et al*. 2009). GLMMs allow for non-normal response distributions where a random effect is included in the model (Breslow and Clayton 1993, Bolker *et al*. 2009).

I initially fit the data using generalized linear models (GLMs) with buffalo or wildebeest counts as the response variable and a categorical variable representing the mowing treatment as the explanatory variable. By omitting the random effect (blocks), I was able to test the assumptions of normality of residuals and variance increasing with the mean (as expected for Poisson distributed data). I assessed the GLMs for overdispersion by calculating the ratio of the deviance to the residual degrees of freedom. I assessed model fit by performing a chi-square goodness of fit test. By evaluating the model overdispersion and fit, I was able to determine whether the link function, dispersion parameter, and variance function were appropriate for each model.

I fit GLMMs for each data set with animal counts as the response variable, treatment as a fixed effect and blocks as a random effect. Poisson variance functions were used for all models except the early dry season models for buffalo and wildebeest which were overdispersed, so a negative binomial variance function was used. The wildebeest early dry season model was also zero-inflated, so a zero-inflated model was used. All of the models fit the data, so the canonical link function was deemed appropriate. The GLMMs for each data set met the assumptions of normality of residuals within blocks, equal variance across blocks, and normal distribution of random effects. I used adaptive Gauss-Hermite quadrature (AGHQ) to approximate likelihood which is recommended for Poisson (or negative binomial) distributed data where the mean number of counts per treatment x block combination is less than 5 and where there are less than 3 random factors (Bolker *et al*. 2009) This technique has been shown to be more accurate than Laplace approximation when conditions allow for its use (Bolker *et al*. 2009).

I tested the effects of the mowing treatment on animal counts by performing Wald Z tests (Wald and Wolfowitz 1940) for each model. I performed tests on data for two species, thus I used a Bonferroni corrected alpha level of .025 for each test (Holm 1979). I compared the between-block variability to the effect of the mowing treatment by comparing the magnitude of the standard deviation of the random effect to the magnitude of the fixed effect.

Effects of Covariates

Important covariates for each species and season data set identified in chapter two are as follows: buffalo wet season = grass principal component 3 (G3), buffalo early dry season = elevation (E), wildebeest wet season = percent woody cover (Wo), wildebeest early dry season = distance to water (Wa), wildebeest late dry season = percent woody cover (Wo). I omitted the buffalo late dry season analysis because there were no continuous variables that appeared to have a strong effect on resource selection. I added these covariates individually to the corresponding GLMMs to identify whether the species relationships with the mowing treatment are affected by other environmental variables.

Before assessing the effects of covariates on the response variable, it was necessary to test for an interaction between the treatment and the covariates. I constructed GLMMs for each data set including the covariate, treatment, and interaction between the covariate and the treatment as fixed effects and blocks as a random effect. I performed Wald Z tests to determine the significance of the covariate-treatment interaction term.

I built a GLMM for each data set that included the mowing treatment and the selected covariate as fixed effects and the blocking factor as a random effect. I performed Wald Z tests on the covariate term for each model to assess the effect of the mowing treatment with the inclusion of each covariate. I calculated the marginal means of animal counts for each treatment level and compared them with the arithmetic means to assess the direction and magnitude of the effects of the covariates on animal counts.

3.3 Results

3.3.1 Environmental response to treatment

Grass Species Composition

Species communities did not differ due to mowing treatment in the wet or early dry seasons (Fig 3.3a, b). This is evident by the fact that the points representing mowed plots (dark red and dark blue) are evenly mixed with points representing unmowed plots (light red and light blue) for all grass species communities (indicated by arrows). In the late dry season, species communities significantly differed between treatments (Table 3.1). Unmowed plots were dominated by *Setaria homonyma* and mowed plots were dominated by *Chloris mossambicensis* and *Setaria sphacelata* (Figure 3.3c).

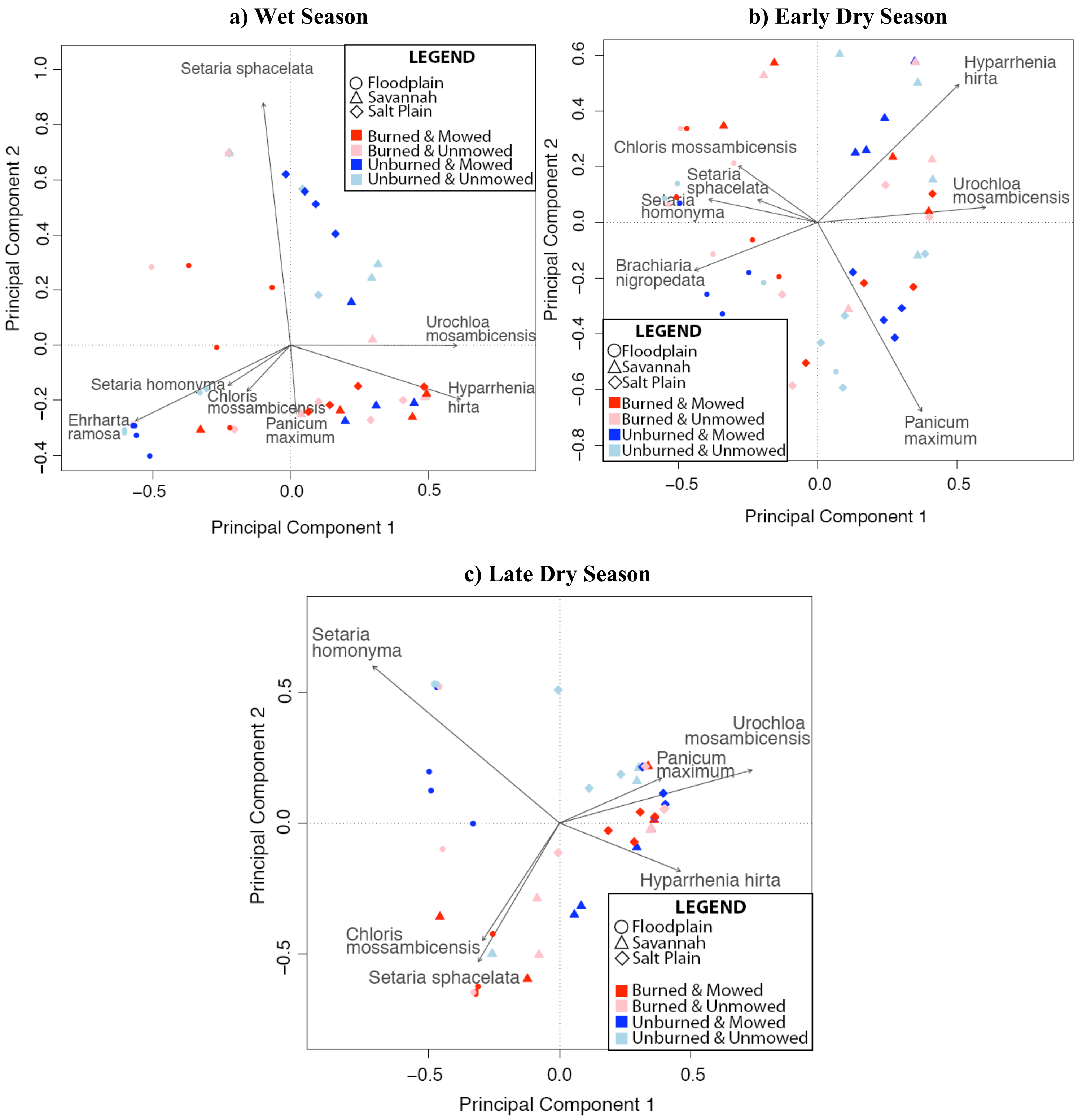


Figure 3.3 Biplots of grass species community ordination showing the first (x-axis) and the second (y-axis) principal components for the wet season (a), early dry season (b), and late dry season (c). Plots symbols represent vegetation types and plot colors represent burned and mowed status.

Grass Quantity

The two variables that represent grass quantity are grass height and grass biomass. The mowing treatment at the beginning of each season resulted in significant differences in grass height and grass biomass at the end of each season (Table 3.1). During all three seasons, grass height and biomass were lower in mowed plots than unmowed plots (Figure 3.4).

Grass Nutrients

The two variables that represent grass nutrients are grass protein and grass greenness. The mowing treatment at the beginning of each season resulted in significant differences in grass protein but no significant difference in grass greenness at the end of each season (Table 3.1). During all three seasons, grass protein was higher in mowed plots than unmowed plots (Figure 3.4).

Soil Nutrients

The three variables that represent soil nutrients are nitrogen (N), phosphorous (P) and potassium (K). The mowing treatment at the beginning of each season resulted in significant differences in phosphorous but no significant difference in nitrogen or potassium at the end of each season (Table 3.1). During all three seasons, soil phosphorous was higher in mowed plots than unmowed plots (Figure 3.4).

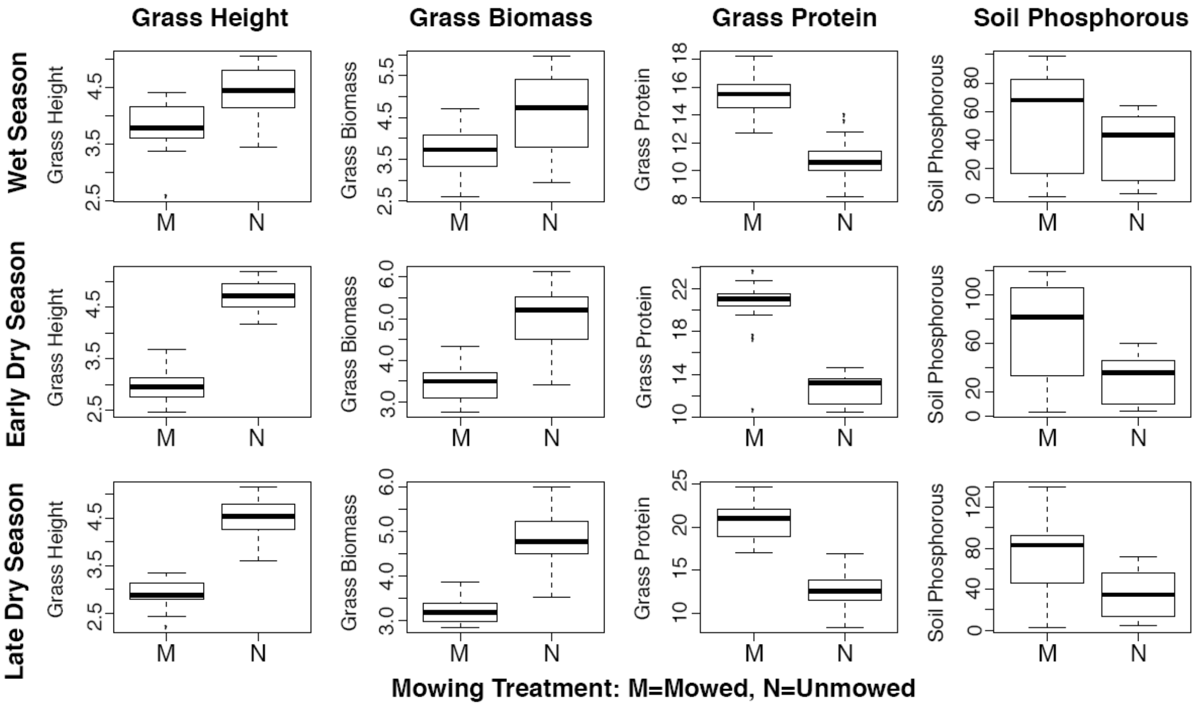


Figure 3.4 Boxplots showing the differences in the distributions of selected environmental variables between treatments.

Table 3.1 Results of t-tests for the environmental variables in mowed vs. unmowed plots across three seasons.

	Wet Season			*Early Dry Season*			*Late Dry Season*		
Variable	t	df	p-value	t	df	p-value	t	df	p-value
Water	0.1169	46	0.9075	0.9019	46	0.3718	0.3221	46	0.7488
Human	-0.3224	46	0.7486	-0.3224	46	0.7486	-0.3224	46	0.7486
Elevation	-0.0293	46	0.9768	-0.0293	46	0.9768	-0.0293	46	0.9768
Woody	-0.4050	46	0.6873	-0.4050	46	0.6873	-0.4050	46	0.6873
Grasspc1	0.3014	45	0.7645	0.0226	46	0.9821	0.4806	46	0.6331
Grasspc2	-1.1090	45	0.2733	0.0235	46	0.9814	-2.2763	46	**0.0275**
Grasspc3	-0.6367	45	0.5276	-0.0176	46	0.9861	-1.2549	46	0.2159
Height	-5.0171	46	**8.30E-06**	-21.1906	46	**<2.20E-16**	-16.1561	46	**<2.20E-16**
Biomass	-4.1772	46	**0.0001**	-9.0792	46	**8.01E-12**	-12.7489	46	**<2.20E-16**
%Greenness	0.6251	46	0.5350	0.4343	46	0.6661	-1.2421	46	0.2205
Protein	12.0334	46	**8.23E-16**	13.5302	46	**<2.20E-16**	13.6418	46	**<2.20E-16**
Soil N	0.3251	46	0.7466	-0.0587	46	0.9534	-0.4902	46	0.6264
Soil P	2.2136	46	**0.0319**	4.3367	46	**7.82E-05**	4.0252	46	**0.0002**
Soil K	0.8366	46	0.4072	0.9996	46	0.3227	1.2142	46	0.2309

Water = Distance to nearest water point
Human = Distance to human habitation
Woody = Percent woody cover
Grasspc1 = First principal component of grass species composition ordination
Grasspc2 = Second principal component of grass species composition ordination
Grasspc3 = Third principal component of grass species composition ordination
Height = Grass height
Biomass = Total vegetation biomass
%Greenness = Percent of green grass
Protein = Grass crude protein
Soil N = Soil Nitrogen
Soil P = Soil Phosphorous
Soil K = Soil Potassium

Note: Bold p-values indicate significance ($\alpha = .05$)

3.3.2 Herbivore response to treatment

The hypothesis that mowing has a significant effect on animal counts for buffalo and wildebeest during three seasons was tested by performing Wald Z tests for each model.

Buffalo

There was no significant difference between buffalo counts in mowed and unmowed areas in the wet season, early dry season, or late dry season (Table 3.2). During the wet and early dry seasons the standard deviation of the random effect (wet=2.22, early dry=1.28) was large compared with the magnitude of the fixed effect (wet=0.89, early dry=0.44). This shows that the between-block variability of buffalo use was large relative to the effects of the mowing treatment. During the late dry seasons the standard deviation of the random effect (2.23) was about equal to the magnitude of the fixed effect (2.12). This shows that the between-block variability was about the same as the effect of mowing treatment.

Table 3.2 Coefficient estimates, standard error of the estimates (σ), z-scores, and p-values for each of the species by season GLMMs without covariates.

	Estimate	σ	z	p
Buffalo - Wet Season				
(Intercept)	-1.2680	0.4811	-2.6360	0.0084
Unmowed	0.6360	0.4171	1.5250	0.1274
Buffalo – Early Dry Season				
(Intercept)	1.0680	0.3640	2.9400	0.0033
Unmowed	-0.8110	0.4660	-1.7400	0.0818
Buffalo - Late Dry Season				
(Intercept)	-1.3938	0.4976	-2.8010	0.0051
Unmowed	0.7537	0.4341	1.7360	0.0825
Wildebeest - Wet Season				
(Intercept)	-0.2731	0.2593	-1.0530	0.2924
Unmowed	-1.1527	0.4735	-2.4340	**0.0149**
Wildebeest - Early Dry Season				
(Intercept)	1.4000	0.3900	3.5900	0.0003
Unmowed	-0.9960	0.4260	-2.3400	**0.0194**
Wildebeest- Late Dry Season				
(Intercept)	-0.1719	0.2485	-0.6920	0.4891
Unmowed	-1.2528	0.4678	-2.6780	**0.0074**

Note: Bold p-values indicate significance (α = .05)

Wildebeest

There was a significant difference between wildebeest counts in mowed and unmowed areas in the wet season, early dry season, and the late dry season (Table 3.2). In all three seasons, wildebeest counts were significantly higher in mowed plots than unmowed plots.

During all three seasons the standard deviation of the random effect (wet=1.33, early dry=1.24, late dry=1.32) was large compared with the magnitude of the fixed effect (wet=0.32, early dry=0.37, late dry=0.29). This shows that the between-block variability of wildebeest use was large relative to the effects of the mowing treatment.

3.3.3 Effects of covariates

I analyzed the effect of the most important continuous covariate (according to the model selection analysis performed in chapter two) for each species and season data set. According to the Wald Z tests, none of the covariate-treatment interaction terms were significant (Appendix B) allowing the analyses of the covariates to proceed for each data set.

The models of buffalo counts which included the treatment effect and covariates showed that the mowing treatment did not have a significant effect on resource selection during the wet season or early dry season (Appendix C). Models of wildebeest counts showed that the mowing treatment did have a significant effect on resource selection during the wet season, early dry season, and late dry season (Appendix C).

The covariates that were included in models of buffalo resource selection for the wet season and early dry season, respectively, were grass species principal component 3 (G3) and elevation. G3 represented a continuum of grass species communities dominated by *Panicum maximum* (low values) to communities dominated by *Hyparrhenia hirta* and *Erharta ramosa* (high values). G3 and elevation were not significantly different in mowed and unmowed areas (Table 3.1) and their distributions appear similar between the treatment levels (Figure 3.5).

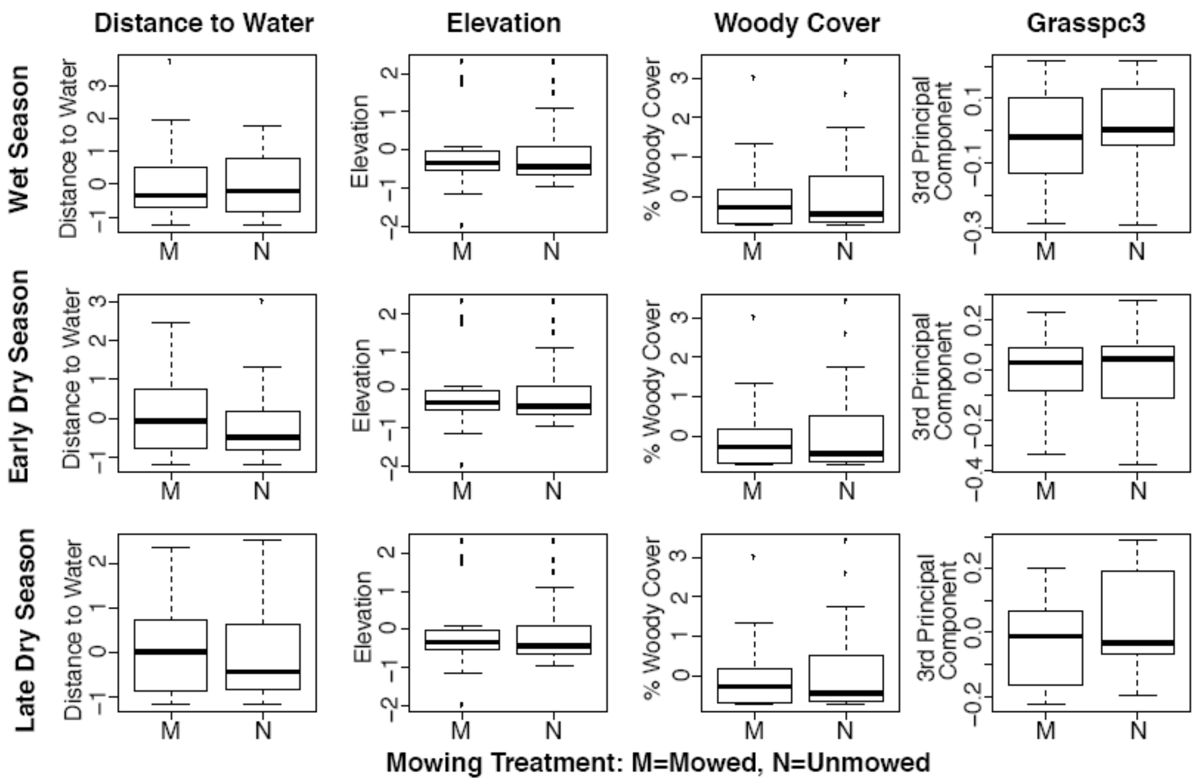


Figure 3.5 Boxplots of model covariates showing the differences in the distributions between mowed and unmowed plots across three seasons. All variables are standardized to μ = 0 and σ = 1.

The covariates that were included in models of wildebeest resource selection for the wet season, early dry season and late dry season, respectively, were woody cover, distance to water and woody cover. Woody cover and distance to water were not significantly different in mowed and unmowed areas (Table 3.1) and their distributions appeared similar between the treatment levels (Figure 3.5).

Buffalo

The arithmetic means of buffalo counts for mowed and unmowed plots during the wet season were 0.69 and 0.67 counts per plot respectively. The marginal means in mowed and unmowed plots, after controlling for the effect of the G3 covariate, remained 0.69 and 0.67 respectively. The mean of the G3 variable was -0.01 in mowed areas and 0.01 in unmowed areas. Buffalo counts were negatively associated with the G3 variable indicating that buffalo had a significant correlation with grass species communities represented by low G3 values (Appendix C).

The arithmetic means of buffalo counts for mowed and unmowed plots during the early dry season were 2.08 and 0.92 counts per plot respectively. The marginal means in mowed and unmowed plots, after controlling for the effect of elevation, were 2.09 and 0.91 respectively. The mean elevation is 40.25m in mowed areas and 40.33m in unmowed areas. Buffalo counts were negatively associated with elevation indicating that buffalo are weakly but insignificantly correlated with low elevation areas (Appendix C).

Wildebeest

The arithmetic means of wildebeest counts for mowed and unmowed plots during the wet season were 0.79 and 0.25 counts per plot respectively. The marginal means in mowed and unmowed plots, after controlling for the effect of elevation, were 0.82 and 0.22 respectively. The mean percent woody cover was 8.1% in mowed areas and 9.5% in unmowed areas. Wildebeest counts were weakly but insignificantly correlated with areas of low percent woody cover (Appendix C).

The arithmetic means of wildebeest counts for mowed and unmowed plots during the early dry season were 4.50 and 1.83 counts per plot respectively. The marginal means in mowed and unmowed plots, after controlling for the effect of distance to water, were 4.40 and 1.93 respectively. The mean distance to water was 555.2m in mowed areas and 609.8m in unmowed areas. Wildebeest counts were not strongly associated with distance to water (Appendix C).

The arithmetic means of wildebeest counts for mowed and unmowed plots during the late dry season were 0.88 and 0.25 counts per plot respectively. The marginal means in mowed and unmowed plots, after controlling for the effect of percent woody cover, were 0.90 and 0.23 respectively. The mean percent woody cover is 8.1% in mowed areas and 9.5% in unmowed areas. Wildebeest counts were weakly but insignificantly correlated with areas of low percent woody cover (Appendix C).

3.4 Discussion

In this study I showed that mowing grass patches significantly affected soil and vegetation properties and increased nutritive quality of the forage in these patches. The short, higher quality grasses attracted wildebeest to these patches during all three seasons. Buffalo preferred unmowed plots in the wet and late dry seasons and mowed plots in the early dry season but the differences in use were not statistically significant. The findings of the mowing experiment were not affected by landscape-scale environmental variables that otherwise may have influenced patch choice.

3.4.1 Environmental response to treatment

It is intuitive to understand that mowing tall grass reduces grass height significantly. The important piece of information that was previously unknown is how quickly the grass in this highly productive landscape could regrow from the start of the growing season in December 2009 until April 2010. The grass during the wet season exhibited the fastest regrowth of all the seasons from a height of 4 cm at the time of mowing to a mean height of 48cm at the end of this season. This is still a significant reduction in grass height compared with a mean height of 89cm in unmowed plots at the end of the wet season. Dry season regrowth in mowed plots was substantially slower with mean heights of 19cm at the end of the early dry season and 18cm at the end of the late dry season. The extent to which herbivores reduced grass height through grazing pressure during each season is unknown.

The Gorongosa ecosystem is extremely productive with tall, high biomass grasslands and savanna. The mowing treatment significantly reduced grass biomass during all three seasons. The thick grass stems that remained after mowing were sparsely distributed which allowed new shoots to grow but the biomass of the regrowth was significant lower than the biomass of the 90m – 120m tall unmowed areas that surrounded mowed patches. In drier climates, such as Serengeti and Arusha National Parks, Tanzania, well-established grazing lawns have a thick, productive grass layer with a high biomass to height ratio relative to the surrounding taller grasses (McNaughton 1976, 1984). In these areas, it is not uncommon for grazing lawns to be higher in biomass than underutilized areas.

The mechanical action of clipping grass stems in a patch has multiple effects on grass nutrients, specifically grass protein. Removing the canopy of tall grasses allows sunlight to penetrate to the soil level which allows seeds to sprout and grow and clipped grasses to regenerate. New shoots are high in protein and easily digestible (Karki *et al*. 2000). New shoots have a high leaf to stem ratio and leaves have a higher protein content than stems which make them a more desirable plant part for consumption by grazers (Sinclair 1977). Partial defoliation of plants can increase photosynthesis and access to sunlight, thus, increase growth rates of new leaves (Detling *et al*. 1979, McNaughton 1983). A positive feedback loop can occur in grazing lawns whereby the high protein content of forage attracts herbivores that defecate and urinate, thereby fertilizing the soil in the patch, which increases protein content of grass and stimulates new growth (Hobbs 1996).

Soil phosphorous was significantly higher in mowed than unmowed plots during all seasons. Mowed plots attracted higher numbers of herbivores than unmowed plots which input nutrients into the soil via defecation and urination (Jaramillo and Detling 1988, Day and Detling 1990). Soil phosphorous is a key nutrient for plant growth, second only to nitrogen, (Schachtman *et al.* 1998) and may increase available phosphorous content in grass which is an important nutrient for herbivores (McNaughton 1988, McNaughton and Banyikwa 1995).

3.4.2 Herbivore response to treatment

Buffalo and wildebeest responded differently to mowing treatments because they are adapted to feed on vegetation in different ways. Wildebeest have a wide muzzle and teeth adapted for cropping very short grass close to the ground (Bell 1971, Estes 1991, Murray and Illius 2000). Their wide muzzle allows them to maximize food intake per bite which conserves energy (Arsenault and Owen-Smith 2008). Wildebeest have been shown to prefer to graze on short grass patches over long grass and the results of this study further support this.

Buffalo have a wide muzzle which allows them to graze on short grass when necessary but their stiff lips prohibit them from grazing on grass shorter than 5cm (Estes 1991). Their prehensile tongues allow buffalo to grab long grass clumps and their large premolars are used to grind course, fibrous grass (Macandza *et al*. 2004, Codron 2008). The results of this study indicate that buffalo do not exhibit a significant preference for mowed or unmowed patches during any season. In terms of grass height and biomass, buffalo may not have exhibited a strong preference for short grass patches, as wildebeest did, because buffalo are adapted to take advantage of long and short grass patches depending on their needs. Buffalo are adapted to digest low-quality grass because microorganisms break down fibrous plant tissue in their rumen through fermentation before passing it to the gut for further digestion (Estes 1991).

Although buffalo patch use did not show statistically significant trends, it is important to note that buffalo used unmowed patches more during the wet and late dry seasons and used mowed patches more during the early dry season. A possible explanation for this trend is that rainfall was lowest during the early dry season which may have rendered the tall grasses too low in nutritional value for buffalo to select them. During the early dry season, mowed patches were 7.9% higher in protein than unmowed patches which may have been an important factor in buffalo patch selection. Although grass protein was higher in mowed patches than unmowed patches during the late dry season, grass greenness was lower in mowed areas which may have influenced buffalo selection of unmowed patches.

Grass protein is a limiting factor in nutrient intake for many African ungulates including wildebeest and buffalo (Sinclair 1974, Sinclair 1977, Seagle and McNaughton 1992, Murray 1995, Prins 1996). Grass declines in protein content with age, and tall, old grass has a very low protein value per bite compared with short, young grass (Prins and Beekman 1987, Beekman and Prins 1989). Herbivores must always balance between energy expenditure and nutrient intake by obtaining the most nutrients for the energy spent during foraging and digestion (Bergman *et al*. 2001). Grazing lawns are optimal resources for those species, such as wildebeest, that are well adapted to utilize them. The mouth morphology of buffalo may deem them incapable of obtaining enough grass intake per bite on very short grass patches to support their nutrient needs. During dry periods, when resources are scarce, buffalo may utilize short grass patches if the nutrient content in these patches counteract the lower food intake rate.

The results of this study exhibit that mowed patches had significantly higher soil phosphorous than unmowed patches. Soil phosphorous influences phosphorous content in grasses which is an important nutrient for both wildebeest and buffalo, especially during pregnancy and lactation (McNaughton 1988, McNaughton and Banyikwa 1995). Wildebeest utilized this resource during all seasons while buffalo only utilized high-phosphorous patches during the early dry season when resources were scarce.

3.4.3 Effects of covariates

The landscape-scale environmental variables that were used as covariates were not significantly different between mowed and unmowed areas. These covariates were then included in models with the mowing treatment variable to assess if these environmental factors influenced buffalo and wildebeest patch use. Since the values of the environmental factors were relatively uniform between patch types (mowed vs. unmowed), it was found that there were no strong effects of landscape-scale factors on patch use. These results indicate that it is appropriate to make inferences about patch use by buffalo and wildebeest in terms of patch-scale resources without including landscape-level resources.

3.5 Conclusion

This study indicates that wildebeest will select short grass lawns when they exist in a matrix of tall, nutrient poor grassland and savanna. Wildebeest are highly adapted to utilize these grazing lawns to their maximum potential by efficiently extracting food resources. Buffalo, in contrast, are generalist herbivores that are adapted to graze on both short and tall grasses but may not feed on short grasses with maximum efficiency due to morphology restrictions. As a result, buffalo do not have strong patch-level preferences for grass height in the Gorongosa landscape. They appear to utilize tall grass areas when resources are abundant and short, nutritious grasses when resources are scarce.

Many studies on wildebeest and buffalo resource use and grazing lawn dynamics were performed in semi-arid, largely short grass ecosystems of East Africa where these species have been present for many decades. This study is unique in that questions about patch selection are placed in the context of animals reintroduced to an altered ecosystem dominated by tall grasses. Understanding how these large grazing species respond to patch-level changes in vegetation structure in a tall grass ecosystem is an important contribution to the current knowledge set about herbivore resource selection.

Additionally, this knowledge is important for informing conservation decisions about stocking densities of herbivores and the utility of patch-scale manipulations in tall grass ecosystems. It is clear that the Gorongosa ecosystem has a long way to go to restore large grazer populations to the densities necessary to begin shifting the ecosystem to a short grass state. Grass growth in this highly productive ecosystem is too fast even for concentrated groups of grazers to independently maintain small grazing lawns at current wildlife densities. This study indicates that wildebeest will aggregate in and potentially maintain grazing lawns in the Gorongosa landscape if herbivore densities increase either naturally or via future reintroductions.

This study creates a foundation for future studies in Gorongosa National Park on consumption rates and the natural establishment of grazing lawns. Future studies could also examine the predicted herbivore densities necessary to shift tall grasslands to an alternative stable state, as well as the changes in grass species, structure, and quality of grazing lawns at various levels of establishment.

4 Conclusion

4.1 Summary

Studies of animal resource selection are essential to understanding the basic ecology of a system. Scientific publications are rife with studies of resource selection in well established research sites with large animal concentrations, such as Serengeti National Park in Tanzania (Seagle and McNaughton 1992, Wilmhurst *et al.* 1999) and Kruger National Park in South Africa (Broomhall *et al.* 2003, Redfern *et al.* 2003, Grainger *et al.* 2005). Studies of resource selection by large mammals reintroduced at low densities to an altered landscape are rare (Knapp *et al.* 1999, Carol *et al.* 2003). Trends in resource selection that apply to a productive, densely-populated landscape may not apply to a sparsely populated landscape with poor food resources.

This study identified seasonal trends in resource selection by two species of herbivores, buffalo and wildebeest, of high conservation concern in an ecosystem altered by the loss of these large herbivores. The findings supported the common assertion that wildebeest select for patches of short, protein-rich grass where available in open areas that are close to water. The findings on buffalo resource selection show that buffalo used resources differently depending on the season. Grass height was only an important factor in the early dry season when resources were scarce. During the late dry season, unmowed areas in salt plain habitats that had previously been burned offered forage with high percent green grass. During the wet season, when food resources were abundant, buffalo selected tall grass areas based on grass species preferences.

4.2 Limitations of this study

Performing large-scale experiments in Africa is not without its challenges. The first unpredicted challenge I faced was with the establishment of an experiment to address the effects of patch burning on grazer use and consumption. After four months of data collection in the field, this experiment was burned in an uncontrolled wildfire. The study described in this thesis was conceptualized and realized after the occurrence of this fire.

The present study utilizes burned and unburned areas as part of the heterogeneous landscape in which the mowing experiment was designed.

I faced two unforeseen challenges in the execution of the mowing experiment. The original design of this study included an estimate of grass consumption in mowed and unmowed plots using herbivore exclosures constructed with rebar and chicken wire. The consumption study failed as over 75% of the exclosures were knocked down by animals, presumably due to poor visibility in the tall grass. I did not anticipate this issue because exclosures constructed in a similar manner in short grass ecosystems had been successful.

The second challenge I faced was in calculating density estimates of buffalo based on line-transect sampling data. Line-transect sampling was performed monthly for eight consecutive months. I collected a sufficient number of wildebeest sightings during all eight months to estimate densities with a high degree of accuracy. However, I rarely recorded any buffalo sightings which made it impossible to calculate accurate densities. These densities were used to assess the correlation between animal densities and dung densities to determine if dung densities could be used as a proxy for animal densities. I found that the correlation between wildebeest densities and wildebeest dung densities was extremely high indicating that it would be appropriate to use buffalo dung counts as an approximation of relative buffalo density between plots.

There are several limitations to this study that I was aware of due to the large scale of this experiment and relatively short time period (one year) available to perform this study. The first limitation is that I was unable to statistically test the effects of burning and vegetation type on resource selection. These areas constituted large blocks in which the plots were established. Treating burn and vegetation type as randomly assigned fixed effects would have been pseudoreplication, therefore, I decided to treat the blocks as random effects.

The second limitation, as a result of the short time span of this study, was that I was unable to examine the conditions necessary for wildebeest and buffalo to maintain grazing lawns. While it was outside the scope of this study, it would have been interesting to assess the establishment of grazing lawns and their long term effects on soil and plant dynamics.

4.3 Conservation concerns

This study was primarily performed to provide park managers with important information for conservation decisions about wildlife and habitat management in Gorongosa National Park. A present concern regarding the restoration of wildlife populations to the park is that low stocking rates, coupled with poor nutrient content of tall grasses, are negatively affecting population growth rates of the reintroduced herbivores. I observed that herbivores within the sanctuary, at present densities, are unable to maintain small, artificially-created grazing lawns. A long-term goal of park managers is to restore the park's vegetation to a short grass state to provide forage for mixed and selective grazers. It is clear that present herbivore populations of the relatively small wildlife sanctuary (5% of the GNP area) are not capable of shifting and maintaining grasslands in alternative short grass state. Without a drastic increase in the rate of large herbivore relocations, reaching the goal of grassland restoration will be a long process.

4.4 Future research

This study was limited in scope due to time and resource constraints but it could be considered a starting point for a long-term study on herbivore-plant interactions in a shifting environment. The establishment of long-term vegetation monitoring plots on grazing lawns and undergrazed areas would allow for a greater understanding of the soil-plant-animal interactions that occur at various stages of grazing lawn establishment.

Future studies may address present impacts of herbivory on grasses by estimating grazer densities, consumption rates, and grass growth rates by season and vegetation type. By understanding the impact of consumption on grass growth, one can predict the required stocking densities of large grazers within the sanctuary that would be necessary to shift and maintain an alternative stable state. The same estimation could be extrapolated to the park outside the sanctuary. This information would be invaluable to inform management decisions and to set targets for future herbivore reintroductions.

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Appendices

Appendix A: Grass species relative abundance - average "number of hits" per plot by strata (vegetation x burn)

Habitat Type	**Season**	*Ehrharta ramosa*	*Setaria sphacelata*	*Setaria homonyma*	*Chloris mossam-bicensis*	*Hyparrhenia hirta*	*Urochloa mosam-bicensis*	*Panicum maximum*	*Brachiaria nigropedata*	*Andropogon spp.*	*Eragrostis rotifer*	*Panicum infestum*	*Unknown Spp*
Unburned Floodplain	Wet Season	55.37	0	29.08	2.58	0	0	1.04	0	0.71	0	0	0
	Early Dry Season	0	1.71	21.96	0.33	0	0	21.08	15.54	0	5.12	0.29	1.92
	Late Dry Season	0	0	37.04	1.38	0.21	0	0	0	0	0	0	0
Burned Floodplain	Wet Season	28.29	27.86	4.62	10.9	0.24	0.9	14.52	0	0	0	0	0
	Early Dry Season	0	18.21	14.29	6.67	0	0	1.75	6.92	0	0	0	0
	Late Dry Season	0	14.5	12.17	4.92	0	0	0	0	0	0	0	0
Unburned Savanna	Wet Season	0.33	8.83	0	0.04	50.71	9.83	0	0	0	0	0	1.33
	Early Dry Season	0	3.29	0	0.68	9.92	4.42	0.1	0	0	0	0	0
	Late Dry Season	0	0.96	0	0.17	5.79	2.54	1.29	0	0	0	0	0
Burned Savanna	Wet Season	0	16.29	2.33	10.25	27.33	11.75	16.33	0	0	0	0	0.083
	Early Dry Season	0	6.25	4.29	3.5	28.83	7.71	7.54	0	0	0	0	0
	Late Dry Season	0	8.08	0.13	2.25	9.25	6.13	2.13	0	0	0	0	0

Habitat Type	**Season**	*Ehrharta ramosa*	*Setaria sphacelata*	*Setaria homonyma*	*Chloris mossam-bicensis*	*Hyparrhenia hirta*	*Urochloa mosam-bicensis*	*Panicum maximum*	*Brachiaria nigropedata*	*Andropogon spp.*	*Eragrostis rotifer*	*Panicum infestum*	*Unknown Spp*
Unburned Salt Plain	Wet Season	0	30.54	0	0	0	7.83	0	1.96	0	0	0	0
	Early Dry Season	0	1.79	0	0	0.29	5.31	20.83	2.37	0	0	0	0
	Late Dry Season	0	0	0.96	0	0.96	7.46	16.21	0	0	0	0	0
Burned Salt Plain	Wet Season	0	0	0.17	3.29	5.42	24.29	18.83	0.79	0	0	0	0
	Early Dry Season	0	3.08	0	0.58	4.88	5.5	20.37	0.88	0.04	0	0	0
	Late Dry Season	0	0	0	1.04	6.38	15.21	8.92	0	0	0	0	0

Appendix B: Model Results from GLMMs of the treatment effect, covariate effect and treatment x covariate interaction.

	Estimate	σ	z	p
Buffalo - Wet Season				
(Intercept)	-1.1226	0.3807	-2.9490	0.0032
Unmowed	0.4107	0.5062	0.8110	0.4172
G3	-2.9333	2.2296	-1.3160	0.1883
Unmowed:G3	-4.1336	2.8291	-1.4610	0.1440
Buffalo - Early Dry Season				
(Intercept)	2.7579	1.3221	2.0900	0.0370
Unmowed	0.1902	2.8125	0.0700	0.9460
Elevation	-0.0537	0.0333	-1.6100	0.1070
Unmowed:Elevation	-0.0248	0.0718	-0.3500	0.7300
Wildebeest - Wet Season				
(Intercept)	0.0308	0.3494	0.0880	0.9300
Unmowed	-0.7874	0.6124	-1.2860	0.1990
Woody	-0.0479	0.0382	-1.2560	0.2090
Unmowed:Woody	-0.1321	0.1669	-0.7920	0.4280
Wildebeest - Early Dry Season				
(Intercept)	1.7124	0.6525	2.6200	0.0087
Unmowed	-0.8103	0.7188	-1.1300	0.2596
Water	-0.0004	0.0007	-0.5500	0.5824
Unmowed:Water	-0.0006	0.0011	-0.5000	0.6137
Wildebeest- Late Dry Season				
(Intercept)	0.1599	0.3602	0.4440	0.6570
Unmowed	-0.8714	0.6222	-1.4010	0.1610
Woody	-0.0565	0.0390	-1.4490	0.1470
Unmowed:Woody	-0.1430	0.1778	-0.8040	0.4210

Unmowed = Mowing treatment level: unmowed
G3 = Third principal component of grass species composition
Elevation = Elevation (m) at each plot
Woody = Percent woody cover of each plot
Water = Distance to nearest water point from each plot

Appendix C: Model Results from GLMMs of the treatment effect and covariate effect.

	Estimate	σ	z	p
Buffalo - Wet Season				
(Intercept)	-1.4228	0.3841	-3.7040	0.0002
Unmowed	0.8780	0.4150	2.1160	0.0344
G3	-5.6427	1.3943	-4.0470	0.0001
Buffalo - Early Dry Season				
(Intercept)	2.9762	1.1706	2.5400	0.0110
Unmowed	-0.7681	0.4791	-1.6000	0.1090
Elevation	-0.0593	0.0291	-2.0400	0.0420
Wildebeest - Wet Season				
(Intercept)	0.1117	0.3398	0.3290	0.7423
Unmowed	-1.1857	0.4777	-2.4820	0.0131
Woody	-0.0645	0.0371	-1.7390	0.0820
Wildebeest - Early Dry Season				
(Intercept)	1.8286	0.6030	3.0300	0.0024
Unmowed	-1.0993	0.4384	-2.5100	0.0122
Water	-0.0006	0.0006	-0.9400	0.3489
Wildebeest- Late Dry Season				
(Intercept)	0.2355	0.3490	0.6750	0.4998
Unmowed	-1.2913	0.4730	-2.7300	0.0063
Woody	-0.0714	0.0378	-1.8920	0.0585

Unmowed = Mowing treatment level: unmowed
G3 = Third principal component of grass species composition
Elevation = Elevation (m) at each plot
Woody = Percent woody cover of each plot
Water = Distance to nearest water point from each plot