Fire ecology in Laikipia, Kenya



A report of the S.A.F.E. project (Scale & Fire Ecology)

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INTRODUCTION

There is wide interest among land managers and conservation biologists in understanding how savanna systems can support such an impressive array of wild grazers. In many parts of East Africa, wildlife serve as key revenue generating sources and ecotourism opportunities are becoming more common on both private and public lands. In Laikipia, Kenya there exists an impressive and diverse mix of wildlife and cattle, with landowners keen to understand the best methods for maximizing a diverse range of animals, both wild and domestic.

The S.A.F.E. (Scale and Fire Ecology) research project set out to understand how the use of prescribed burns in Laikipia, Kenya affects the foraging ecology of wildlife. We were keen to understand whether burning is useful for maintaining wild herbivore populations. In this study we make the assumption that an animal's preference for a burned area would be a good indicator of long-term population responses: if an animal prefers burned areas, through time this will likely translate to an increase in numbers of that species. While there have been numerous studies generally examining how wildlife respond to burning, there has been very little consensus on *which* species prefer burned areas. Therefore, we were particularly interested in testing the ecological theories predicting that grazers of smaller body size would make use of burns more than larger species.

While this report does not seek to be an exhaustive review of the relevant studies and literature regarding fire ecology and grazing, we provide some of the background information, which may be of interest to some land managers. The primary goal of this report is to discuss how the use of fire may be a useful tool for land managers and conservationists in Laikipia, Kenya.

Integrating theories of grazing, fire, and landscape ecology

For decades ecologists have been trying to understand how large numbers of species can coexist feeding on the same food (Hutchinson 1959) and African herbivores have been studied extensively in this regard (Bell 1970; McNaughton & Georgiadis 1986; Ritchie & Olff 1999; Olff *et al.* 2002). In these systems, it is suggested that the coexistence of wild grazers is due to variation in plant quality and quantity, which allows different species to avoid competing for the same kind of food (Belovsky 1997). Smaller animals are constrained to feed on rarer, higher quality items, while large species can tolerate poor quality food which is more abundant

(Demment & Van Soest 1985). These ideas have helped fuel interest in the "heterogeneity" paradigm, where the high herbivore diversity in savanna systems has been attributed to the variation of the quantity and quality of grass that naturally occurs across the landscape throughout the season (du Toit 2003; Owen-Smith 2005a). The following sections present a more detailed argument for the importance of fire in the evolution of savanna grazing systems.

Smaller bodied grazers require higher quality forage

Residents of Laikipia are well aware that the shortly cropped glades are highly preferred grazing spots for many of the smaller herbivores like impala, warthog, and gazelle. Why do smaller bodied animals prefer these grazing lawns? Undoubtedly, they seek refuge in these open areas, in part, to avoid predation. Smaller bodied grazers also prefer these areas for their improved forage quality (though reduced quantity).

Bell (1970) and Jarman (1974) were the first to propose a digestive explanation for the coexistence of herbivores of varying body size, later coined the Jarman-Bell Principle. They suggested that smaller herbivore species require higher quality food than larger species due to their higher metabolic demands, while larger species require greater quantities of food and are more tolerant of lower quality. Although we don't quite know why, smaller animals burn more energy per gram of tissue than larger species. Since their gut size is directly proportional to their body size, smaller animals have to figure out a way to digest food *faster* than larger species. They do this by selecting forage that is easier to digest (higher quality). This is particularly important for herbivores because plant material contains a high percentage of cellulose, which can only be digested by fermenting bacteria in the animal's gut. The best way to digest the cellulose is to increase the amount of *time* the bacteria have to ferment the cellulose. This explains the evolution of digestive structures that seek to increase digestive retention time, like the elongated large intestine of zebras (hindgut fermenters) and the complex fore-stomach of antelope, gazelles, and cattle (foregut fermenters). This further explains why smaller bodied animals are at a disadvantage compared to larger bodied animals. Because their guts are smaller, the fermenting bacteria have less time to digest the ingested cellulose.

Landscape ecology

If the diversity of grazers varying in body size is related to their unique preferences for forage, it is important to understand the key processes that maintain grass heterogeneity at the landscape scale. Theoretical models, based on tradeoffs between grass quantity and grass quality, predict that *for each body size there exists an optimal biomass of grass that maximizes energy intake* (Illius & Gordon 1987; Wilmshurst *et al.* 2000) and that variation in grass heights at the landscape scale can facilitate large herbivore coexistence (Farnsworth et al. 2002). As grass matures, its percentage of cellulose increases which lowers its quality as a food resource for herbivores. Therefore, shortly cropped young grasses are of higher quality than older swards and are often maintained as "grazing lawns" by periodic preferential selection by herbivores (Verweij *et al.* 2006; Archibald 2008).

A key difficulty in testing how grazers of varying body size select food resources is that their preferred foraging patches must occur at spatial scales that are relevant to the species in question. The spatial attributes of food patches, such as size and patchiness, may affect how animals of varying body size perceive food resources (Ritchie 1998), move across the landscape (Wiens et al. 1997), and selectively forage (Laca et al. 1993), leading to the hypothesis that spatial heterogeneity of food resources, at multiple scales, may in itself promote diversity (Ritchie & Olff 1999).

Fire Ecology

Fire-grazing interactions are important processes that promote variability in grass quality and quantity (Archibald *et al.* 2005; Kerby *et al.* 2007). Klop and van Goethem (2008) have recently demonstrated that savanna fires may be influential in generating regular body mass distributions, which suggests that fire processes may confer body- size related constraints on forage acquisition and/or resource perception. This is an important insight, as it is increasingly recognized that fire has influenced the evolution of savanna biomes for millions of years (Keeley & Rundel 2005).

We designed a large scale, replicated study that integrates the above insights from bodysize scaling, landscape ecology, and fire ecology in order to test whether fire induced heterogeneity is vital to the coexistence of grazers of varying body size. We implemented multiple prescribed burns in order to manipulate grass quality and quantity in an otherwise homogenous *Acacia drepanolobium* savanna in Laikipia, Kenya, and measured the response by an entire guild of large herbivores ranging in body size from the 2 kg hare to the 3500 kg African elephant. By varying the size and patchiness of the burns, we avoided selecting a "patch" size biased to a preconceived spatial scale or focal organism.

The S.A.F.E. project was designed to address a variety of questions related to the effects of fire on the ecology of savanna systems. We were interested in the following questions:

Vegetation

- 1. How does burning affect grass species composition?
- 2. How does burning affect grass as forage for grazers (quality and quantity)?
- 3. How does burning affect the amount of grass produced per unit time (productivity)?
- 4. How does burning affect the prevalence of whistling thorn (*Acacia drepanolobium*)?

Grazer response to burning

- 1. How do grazers respond to the re-growth in burned sites?
- 2. Does a grazer's body size influence its use of burned sites?
- 3. Does a grazer's gut type influence its use of burned sites?
- 4. Does the size and pattern of the burn influence grazer use?

EXPERIMENTAL OVERVIEW & METHODS



Study system

The study was performed in the Laikipia District (37°53'E, 0°17'N), a semi-arid *Acacia* savanna that boasts the largest population of wildlife in Kenya's non-protected areas. Land ownership is a mix of large-scale cattle ranches, pastoralist Maasai group ranches, and smallholder agricultural settlements. The impressive diversity and high densities of wildlife in Laikipia has attracted international attention and continues to be an exciting area of research regarding the opportunities and challenges in wildlife conservation in human dominated landscapes.

In the context of a thriving guild of large carnivores which include lion (*Panthera leo*), leopard (*Panthera pardus*), cheetah (*Acinonyx jubatus*), and wild dog (*Lycaon pictus*), the system supports a diverse large herbivore assemblage including elephant (*Loxodonta africana*), giraffe (*Giraffa camelopardalis*), eland (*Taurotragus oryx*), buffalo (*Syncerus caffer*), zebu cattle (*Bos primigenius indicus*), zebra (*Equus burchellii* and *E. grevyi*), waterbuck (*Kobus ellipsiprymnus*), hartebeest (*Alcelaphus buselaphus jacksoni*), oryx (*Oryx gazella*), warthog (*Phacochoerus*) *aethiopicus*), Grant's gazelle (*Gazella granti*), Thomson's gazelle (*Eudorcas thomsoni*), impala (*Aepyceros melampus*), steinbuck (*Raphicerus campestris*), and cape hare (*Lepus capensis*).

The mean annual rainfall varies between 500-650 mm, falling in a tri-modal pattern with wet seasons in April-May, August, and October. The region is underlain by two soil types: black cotton vertisols derived from basaltic lava flows and red sandy loams from metamorphic basement layers. All experimental plots were on homogeneous black cotton communities, where whistling thorn tree (*Acacia drepanolobium*) comprises 97% of the woody layer and the grass

layer is dominated by four major species of C4 grasses, red oat grass (*Themeda triandra*), *Brachiaria lachnantha*, Maasai grass (*Pennisteum stramineum*), and bamboo grass (*Pennisetum mezianum*) (Young et al. 1997). (*It is important to note that the findings of the S.A.F.E. project are applicable to the black cotton soils. We do not suggest that our findings are necessarily relevant to management of the red, sandy soils as we did not burn in these habitats. This will be discussed more in the management section.*)

Experimental design

The S.A.F.E. (Scale & Fire Ecology) project is a large scale collaborative initiative begun in 2004 with the aim of understanding how



Figure 1 Laikipia District is in the western rain-shadow of Mt. Kenya and located directly on the equator. The shaded properties indicate four ranches which collaborated with the author in this experiment. MRC indicates the location of Mpala Research Centre, from which this study was based.

prescribed burning affects the community ecology of savanna systems in East Africa. The project arose out of conversations with a variety of landowners in Laikipia, Kenya whom expressed interest in understanding the role that fire plays in the management of their properties. Out of these conversations, I developed a project which was a partnership with four different cattle ranches with similar densities of wildlife: Mpala Ranch, Jessel Ranch, Segera Ranch, and Ol Pejeta Conservancy (from north to south as shown in Figure 1).

In addition to the partnerships with landowners in the region, Nathan Gregory from Princeton University was a partnering collaborator and was instrumental in implementing the project. Nathan studied how birds communities responded to burning. Additionally, Dr. Jesse Njoka and his Masters student, Isaac Kimathi, (University of Nairobi) supported the project and collected valuable data regarding the productivity of grasses in burned and unburned areas. Mpala Research Centre, located on Mpala Ranch, served as the project's base and was instrumental in providing logistical support.

Methods

We burned a total of 18 plots, which varied in both their total area and their patchiness as shown in Figure 2. Total burn area varied at three levels: 1, 9, and 81 hectares. Each size class was burned at two levels of patchiness: "continuous" and "patchy". All burns were completed at the end of the dry season in February/March before the long rains. A complete replicate of treatments was implemented in March of 2004 and two replicates were added in February/March of 2005, from which data were collected for 15 months after burning. Due to the rigorous burning protocol necessary to burn the 81 ha patchy plot, this treatment was not further replicated. The 9 hectare continuous and 81 ha continuous treatments were replicated 4 times,

the 81 hectare patchy burn 1 time, and all remaining treatments three times. Study sites were spread across central Laikipia on the four cattle ranches which were characterized by similar densities of wildlife, homogeneous black cotton soils, and dominance by an *Acacia drepanolobium* over-story. Burns were spatially located as far apart as possible to maximize treatment independence; most burns were between 5–15 km apart, with several burns approximately 1 km apart.



Figure 2. Creation of fire breaks on an 81 hectare patchy burn on Segera Ranch using backing fires (Photo by R. Sensenig)

Prescribed burning

In 2004, a two-day training course in fire ecology and prescribed burning techniques was offered to more than 20 field assistants at Mpala Research Centre (MRC). During the 2005 year this training was augmented with a one day refresher course to prepare for the 2005 burn season. With the help of MRC field assistants and personnel from each of the collaborating ranches, each plot was burned using standard prescribed fire techniques. During the morning hours (when wind was low, humidity high, and air temperatures cool) we used backing fires to create firebreaks (typically 10-20 meters wide) on the down wind side of the plots (Figure 2). In the midmorning we used head-fires (fires moving with the wind) to burn the interiors of the plots.

For all burns completed in 2005, ceramic tiles marked with welding paints (Tempilaq G) were hung from whistling thorn trees 0.5 m off the ground throughout the burned sites to estimate burn temperatures. Each color of paint has a specific melting temperature and therefore burn temperatures can be estimated after the fire by collecting tiles and assessing which colors of paint melted.





(b) 81 ha patchy burn

Figure 3. Experimental design (Fig. 1a) with burns replicated at two levels of "patchiness" (continuous and patchy) and three sizes (81, 9, and 1 hectares). In the 81 ha size classes, the layout of 4 meter wide dung transects is shown. The shaded areas indicate burned areas (solid black transects) and the white areas indicate unburned areas (grey/black dashed transects). Within each treatment size class, *continuous* and *patchy* treatments comprise the same total burned and unburned area. The small dotted line represents perpendicular *control* transects that extend into the unburned matrix for all treatments (only shown here for the 9 ha patchy burn). Aerial photo (Fig. 1b) of an 81 hectare patchy burn.

Vegetation characteristics

In order to see if grazers were using (or avoiding) burned areas because of changes in grass quality and quantity, we measured the following attributes for grass species: grass biomass, percent live leaf, normalized difference vegetation index (NDVI), acid detergent fiber (ADF), crude protein (CP). More descriptions of these variables are found below.

Grass biomass and percent live

In the burned and unburned areas in each plot, the grass biomass and percent live leaf was estimated simultaneously with dung data using a canopy intercept method with a 1 m vertical 4-point pin frame. Pin frame placement was every 20 meters along the dung transects (every 50 m in the 81 ha sites). Within each pin frame all contacts by each plant species (grasses and forbs) for live leaf, dead leaf, and stem were counted. For a subset of these plots, we clipped all the grass and forbs after counting pin hits. Using this relationship we were able to mathematically determine a relationship between pin hits and grass biomass. We therefore used "pin hits" to calculate grass biomass for the remainder of the study. We also used the pin hit data to calculate the percentage of live leaf, percentage of dead leaf, and percentage of stem, as these attributes are important factors in affecting which grazers prefer the grass,

NDVI: An estimate of relative rainfall

For each survey period the normalized difference vegetation index (NDVI) was calculated by averaging two locations immediately outside each burn plot. NDVI is a measure of how green the foliage is and can indicate generally how much relative rainfall an area receives. These data come from Mpala Research Centre and were derived form MODIS satellite images (250 m resolution) taken every 16 days.

Grass forage quality using NIRS

We used near infrared reflectance spectroscopy (NIRS) to evaluate grass quality of clipped samples from a subset of transects in each plot. Crude protein (CP) and acid detergent fiber (ADF) were estimated for clippings of the three dominant grasses. Crude protein is an estimate of nitrogen in plant tissue that is derived from protein and some non-protein nitrogen (such as in nucleic acids). Acid detergent fiber is inversely related to forage quality as it

indicates the relative amount of cellulose and lignin in plant tissue, both of which lower forage digestibility. Forage with high CP and low ADF values are of the highest quality for herbivores.

Grass clippings were analyzed from 8, 16, and 20 locations in each of the 1, 9, and 81 hectare plots during the following survey periods: 40 days and 450 days after burning in plots burned in 2004 and 70 days, 150 days, and 500 days after burning in plots burned in 2005. Samples were first air dried in the shade; dried in a charcoal fueled drying oven for 6 hours on 2 consecutive days; hand



separated by live leaf, dead leaf, and stem; and ground to 1 mm on a Wiley Mill. A total of 1850 ground grass samples were then scanned in a near infrared scanning spectrophotometer (6500; NIRSystems, Silver Spring, MD, USA) at the University of California, Davis. Average plot quality indices were calculated for both burned and unburned areas by multiplying the ADF and CP means for live leaf, dead leaf, and stem in each plot by the percentage of each plant part present in that plot (derived from the pin frame data).

Grazer use of burned sites

Grazer preference for burned sites was assessed using permanent 4 m wide dung transects spaced every 20 m, 80 m, and 200 m in the 1, 9, and 81 hectare burns respectively. Dung was surveyed continuously along transects, recorded by species at ten meter intervals, and subsequently crushed to avoid recounting in the next survey. Cattle and buffalo dung were grouped as one category as they are extremely difficult to differentiate. When dung was found in a midden (i.e. Grant's gazelle, impala, and hartebeest), the total number of dung piles was estimated using differences in color, freshness, and shape.

Following burning, surveys were completed after approximately two, five, eight, and fifteen months. Dung transect grids were identical for patchy and continuous burns, with similar search intensities in burned and unburned areas (Figure 1). To measure wildlife use in unburned areas near the treatments, two control transects were laid out perpendicular to each plot extending into the unburned matrix 200, 400, and 1200 meters in the 1, 9, and 81 hectare burns,

respectively. To ensure our results were not influenced by the fact that dung is easier to find in burned areas, data were corrected to account for observer bias using multiple re-counts.

For each plot, we calculated a burn preference index for each species (i) as the ratio of dung in burned areas divided by the combined total of dung in burned areas plus dung in the neighboring unburned control transects. Dung means for each plot were divided by the number of days since the last survey to account for variability of time during which dung accumulated.

burn preference	dung p	dung per m ² per day in burned areas		
index _i =				
	2	2		

(dung per m^2 per day in burned areas + dung per m^2 per day in control transects)

The index ranges from 0-1, where 0 equals complete avoidance of burned areas and 1 indicates complete preference for burned areas. When a species was missing entirely from a plot (i.e. missing in burned and control transects), this species/plot pair was excluded from analysis. Species were only included in the analysis if they occurred in at least 25% of the burn plots (Thomson's gazelle was thus excluded). Because we were interested in how grazers responded to changes in grass quality, the two pure browsers in the region (giraffe and steinbuck) were also excluded from the analysis. Cattle (and thus buffalo) were not included in the analysis regarding burn preference because they are continually tended by local herders and do not select among resource patches independently.

RESULTS



Fire temperatures

Fire temperatures were measured in burns completed in 2005. Temperatures were lower in plots located on Ol Pejeta Ranch because of lower initial grass biomass due to higher wildlife and cattle densities. Smaller plots burned at slightly lower temperatures than larger burns. The average burn temperature for all plots was 305 degrees C (582 F).



Figure 4. Mean temperature estimates for burns completed in 2005. Values were obtained by averaging multiple temperature tiles placed in the grass layer before burning. OL9P05 was a cool burn due to rain that began during burning and OL1P05 and OL1C05 burned incompletely due to reduced grass biomass. See Figure 3 and associated table for further description of plot names. J = Jessel Ranch, MP = Mpala Ranch, OL = Ol Pejeta Conservancy, SG = Segera Conservancy

Laikipia experiences high variability in rainfall in space and time

Typical of savanna systems, we observed high variability in rainfall in both time and space as measured by the near difference vegetation index (NDVI). As mentioned previously, NDVI is a measure of greenness and can indicate relative amounts of rainfall. A slight north-south gradient of increasing rainfall was evident, though this pattern was not consistent during all survey periods (Figure 5).

The striking variability in rainfall is evident in Figure 6 where NDVI values are shown for representative plots located on Ol Pejeta Ranch for the duration of the study. A distinctly trimodal rainfall pattern is evident with a long rainy season followed by two shorter rainy seasons. Additionally it is important to notice the high *spatial* variability in rainfall, evident when comparing NDVI values for a variety of plots at a given date. This variability was vital to our study as it enabled us to measure how animals responded to both burned and unburned sites that were markedly different in vegetation attributes at any given time.



Figure 5. Average grass greenness as measured by NDVI for all plots by survey period and ranch. These data in general confirm a rainfall gradient that runs from north to south (with Ol Pejeta ranch receiving the highest rainfall levels), but also indicates that in both years Ol Pejeta received less than average rainfall immediately after burning (surveys 1 and 2).



Figure 6. The Laikipia system experiences high variability in rainfall as demonstrated in the normalized difference vegetation index (NDVI) shown here. NDVI measures grass greenness and is a rough surrogate for rainfall. This graph shows plot NDVI values from burns completed on Ol Pejeta Ranch in 2005 for 550 days since burning. All burns were completed during the dry season in February of 2005.

VEGETATION RESPONSE TO BURNING

Biomass of grass re-growth is lower in burned areas (mainly due to decreases in stem and dead leaf biomass)

The variability in rainfall across the ranches and throughout the study led to high forage variability in quality and quantity. Total grass biomass of all species combined was 20-60% lower in burned areas than in unburned areas during all periods survey (Figure 7). Soon after burning, grass re-



Figure 7. Plot means (+/- SE) of total grass biomass as a function of days since burning for burned areas (filled circles) and unburned areas (open circles). The tri-modal pattern of rainfall in this system is evident in the pattern of the normalized difference vegetation index (NDVI).

sprouted in burned areas and attracted grazers to the high quality leafy material, which further maintained the area as a grazing lawn. Burning removed senescent stem material and dead leaves creating foraging areas of low biomass, but high quality. As measured using total pin hits, the amount of live leaf tissue was on average 24% lower in burned patches than in unburned patches, though only statistically significant during the first survey (Table 1).

The major difference between the biomass of grass material in burned and unburned plots was in the amounts of dead leaf and stem. The amount of dead leaf and stem was on average 58% and 57% lower in burned patches than unburned patches, respectively, a pattern that was highly significant during all survey periods including the fourth survey 480 days since burning (Table 1). Strikingly, the biomass of *live leaf* material was very similar in burned and unburned areas. This has profound effects for grazers, because in burned areas the forage is almost entirely live leaf, which makes for a high quality bite of food, particularly for the smaller bodied animals as mentioned later in this report.

	•	• · ·		• •		
plant part	survey	mean pin hits burned	(per 30 cm ^{2)} unburned	F ratio	df	p value
live leaf	1	5.8 +/- 0.67	9.5 +/- 0.54	17.58	47	< 0.0001
	2	6.6 +/- 0.90	8.4 +/- 0.81	1.79	53	0.19
	3	7.5 +/- 0.48	8.7 +/- 0.43	2.82	53	0.099
	4	5.4 +/- 1.17	6.6 +/- 0.93	0.6	39	0.44
dead leaf	1	0.7 +/- 0.15	6.1 +/- 0.33	199	47	< 0.0001
	2	4.3 +/- 0.57	10 +/- 0.70	28.4	53	< 0.0001
	3	3.8 +/- 0.58	8.1 +/- 0.53	25.3	53	< 0.0001
	4	3.7 +/- 0.54	5.7 +/- 0.47	6.9	39	0.013
stem	1	1.0 +/- 0.14	4.5 +/- 0.26	140	47	< 0.0001
	2	2.3 +/- 0.45	4.9 +/- 0.29	25.2	53	< 0.0001
	3	2.4 +/- 0.28	4.8 +/- 0.30	31.25	53	< 0.0001
	4	1.9 +/- 0.54	3.3 +/- 0.32	5.6	39	0.023

TABLE 1. Changes in grass plant parts due to burning for all grasses combined

Table 1. Statistics for pin hits of live leaf, dead leaf, and stem in burned patches and unburned patches during the four different surveys. Multiple pin placements were first averaged to obtain plot means and degrees of freedom represent replicates at the plot level.

All four grass species also had significantly less percentage of stem material immediately after burning (Figure 8), *Pennisetum mezianum* (bamboo grass) exhibited the most dramatic reductions in its total percentage of stem in burned areas and in this regard was not statistically different from *T*. *triandra* (red oat grass), which



Figure 8. Mean percent stem (+/- SE) during the final survey 480 days since burning for the four major grass species in burned (shaded) and unburned (white) patches. brach = *Brachiaria lachnantha*, mez = *Pennisetum mezianum*, stram = *Pennisteum stramineum*, them = *Themeda triandra*

showed only marginal declines in its percentage of stem in burned areas. *P. mezianum* and *Pennisetum stramineum* (particularly near termite mounds) were both cropped low to the ground and did not extend lengthy stem structures in burned areas, as is typical for them in unburned

areas (R. Sensenig, personal observation). These patterns may help explain why *T. triandra* increased in dominance in burned areas.

Despite lower standing biomass in burned areas, grasses are more productive in burned areas than unburned areas

Isaac Kimathi, an MS student from the University of Nairobi, worked collaboratively with the S.A.F.E. project to measure how burning affects grass productivity. By using moveable cages, Isaac was able to measure how much new plant material is produced per m² during a given unit of time. Burning can increase plant productivity for a number of reasons, including access to increased sunlight, a flush of nutrients, warming of the soil due to increased absorption of sunlight, and plant compensatory responses due to loss of aboveground tissue. In this regard the low standing biomass levels in burned areas is somewhat misleading because through time the productivity may actually be higher than in unburned areas.



Figure 9. Plant standing biomass is significantly higher in unburned areas, yet plant productivity (grams per m^2 per year) is much higher in burned areas than unburned areas



Figure 10. Grazing exclosure showing the biomass of grass removed by herbivores in a burned site.

Red oat grass (Themeda triandra) becomes more dominant with burning

The four most dominant grasses in our study were red oat grass (*Themeda triandra*), Maasai grass (*Pennisetum stramineum*), bamboo grass (*Pennisetum mezianum*), and (*Brachiaria lachnantha*) (Figure 12). See Appendix C for pictures and further descriptions. Each of these species has unique structural growth patterns with the *Pennisetum* species typically having higher percentages of low quality stem material. The *Pennisetum* species are upright growing grasses with large portions of their biomass dominated by stem material. Both *T. triandra* and *B. lachnantha* are comprised of less stem

material. Burning acts to create plant part percentages that are more similar between the species.

When the biomass of the four species of grass was analyzed separately, there were notable differences in grass abundance in burned areas as expressed by the ratios of burn/unburn pin hits for live leaf, stem, and dead leaf (Figure 13). Red



Figure 11. Photo from a 1-hectare burn site showing the prevalence of *Themeda triandra* approximately 1 year after burning. Patrick Etelej, one of the project's field assistants, is kneeling and holding several of the abundant stems of *T. triandra*.



Figure 12. Mean percentages (+/- SE) of the four dominant grasses in unburned and burned patches at the conclusion of the experiment showing that Red Oat Grass increased in dominance after burning.

oat grass was the only grass species that had similar quantities of live leaf, dead leaf, and stem in burned and unburned patches by the end of the experiment (Figure 13). In fact the biomass of red oat grass <u>live leaf</u> material was higher in burned areas than unburned areas.



Figure 13. Mean ratios (+/- SE) of pin hits in burned patches divided by pin hits in neighboring unburned patches from 18 replicate plots. A pre-burn survey is indicated by -30 days. Dashed lines indicate equal pin hits in burned and unburned patches and therefore demonstrate when burned and unburned biomass values are equivalent.

This confirms the general anecdotal evidence that Red Oat grass becomes more abundant in burned areas.

As shown in Figure 14, there was significant variability in pre-burn percentages of *T*. *triandra* across the ranches, which was positively correlated with relative herbivore density (as measured by total dung

density). Other studies have found that Т. triandra decreases in response to increasing grazing pressure (O'Connor 1994, 1996). The positive correlation in our study may result from the fact that Themeda *triandra* is intolerant of litter accumulation and declines in the absence of disturbance. In the black cotton soils grass biomass levels reach high levels due to the high water holding capacity of clay soils.



Figure 14. Percentage of total grass cover by *Themeda triandra* as a function of total dung density of all grazers combined. Points are means for each of the four ranches separately for unburned areas (open circles) and burned patches (filled circles). The linear fit for unburned patches is indicated by the bold line, a quadratic fit includes all burned and unburned points together. Unburned data included unburned patches, control transects, and control plots. (Ol Pejeta - squares, Jessel - triangles, Segera - diamonds, Mpala - circles).

Perhaps the positive correlation between grazer dung and percent *T. triandra* lies in the ability of grazers to maintain an open, light-rich environment by reducing the biomass of co-dominants.

Burning also increased the relative abundance of *Themeda triandra*, however increases were marginal if *T. triandra* already dominated the vegetation community before the experiment and the increase in *T. triandra* in burned areas was also positively correlated with dung density, as found in the unburned areas (Figures 14). In fact, when controlling for total dung density, the

effect of burning on percentages of *T. triandra* was no longer significant. There appears to be a maximum percentage of *T. triandra* (~ 35%) after which burning and higher grazing intensities no longer increase its prevalence, and in fact, decrease its community percentage. This is consistent with a grazer driven hypothesis in that in areas where *T. triandra* is already very high, grazing pressure on nearby co-dominants is insufficient to alter the community composition, perhaps because grazers cannot preferentially select other grasses.

These patterns parallel the conclusions of Coughenour et al. (1985), who have suggested that in the Serengeti *T. triandra* is able to survive amidst high densities of large herbivores, only when in the presence of short-grass species which are more palatable. They suggested that *Themeda*'s higher stature, lower leaf:stem ratios, high percentage of flowering culms, and sparser canopy may make it less suitable for grazers than the short grass species. In the black cotton soils of Laikipia, high biomass levels of grass accumulate in the absence of fire, creating environments where species such as *P. mezianum* and *P. stramineum* obtain high percentages of stem making them structurally difficult to consume. Fire may temporarily create short-grass grazing lawns, in which *T. triandra* is no longer preferentially selected because grazing pressure is more evenly distributed among all grass species.

Grass re-growth in burned areas is higher in quality (less cellulose)

As found in other studies, we found that grass quality is generally inversely related to biomass because as a plant matures its tissue becomes richer in cellulose (Figure 15). Cellulose is resistant to breakdown and only digestible by fermenting bacteria found in a grazer's gut. As plants mature their cell walls thicken and the percentage of stem tissue increases, both of which increase the amount of cellulose and lower forage quality. Similarly, crude protein (the amount of nitrogen) was higher in burned areas compared to unburned areas, but only statistically significant during the first post-burn survey.

As expected, we found plant quality was higher in burned areas: acid detergent fiber was 10-18% lower in burned areas compared to unburned areas. However, we also found high variability in ADF across our study sites (Figure 16). The amount of nitrogen (crude protein CP) in the grasses was improved immediately after burning, but by the second survey CP was the same in burned and unburned sites. The improved quality of grasses in burned areas is due to increased leaf:stem ratios, concentration of



Figure 15. Plant quality declines as a plant gets taller and more mature, the 'forage maturation hypothesis.' Here plant quality is measured as acid detergent fiber (ADF), a measure of the amount of fiber/cellulose in the

available nutrients over less tissue biomass, and plant rejuvenation (Van de vijver et al. 1999).

The grass quality data shown in Figure 16 is calculated by averaging the CP and ADF values for each of the respective *plant parts* (live leaf, dead leaf, stem) by the relative abundance of that plant part in the site. In other words, since the grass growing back in a burned site is higher in leaf material and very low in stem material, this leads to overall quality that is much higher. However, the improvements in grass quality in burned areas is not only a result of increases in the *percentage* of live leaf, but also because the individual plant parts are of higher quality as shown in Figure 17.



Figure 16. Plot means for crude protein (CP) and acid detergent fiber (ADF) as a function of days since burning for burned patches (filled circles) and unburned patches (open circles). Error bars indicate standard errors and p values are from ANOVA's testing whether there is a difference between burned and unburned values separately for each survey period. CP was higher in burned areas only during the first survey, ADF was lower in burned sites during the entire study.



Figure 17. Quality of grass tissue as measured by acid detergent fiber and crude protein by plant part for burned (gray bars) and unburned (white) areas. The big arrows indicate the direction of increasing quality. As ADF (cellulose content) decreases, the quality of the grass increases. As CP (amount of protein) increases, the quality of the grass increases.

Grass quality varies by plant species

There is much anecdotal evidence to suggest that Red Oat Grass (*Themeda triandra*) is a preferred forage for cattle and wildlife. This is one of the explanations for why *T. triandra* becomes more common in

burned areas, because the non-Themeda species increase in quality and "absorb" more of the grazing pressure.

Contrary to these predictions, we did not find major differences in the hierarchy of plant quality attributes between the four dominant perennial grass species in burned sites as compared to unburned sites (Figure 18). We predicted that the high "palatability" of T. triandra in unburned areas may relate to its low percentage of stem material compared other coto



Figure 18. Acid detergent fiber (ADF) and crude protein (CP) means (+/-SE) for "whole plant" values calculated by weighted averaging of live leaf, dead leaf, and stem CP and ADF values relative to their percentage in plot. Letters indicate significant differences between LS means (Tukey's HSD, p < 0.05) from separate linear mixed models with *plot* as random effects and *grass species*, *NDVI*, and *NDVI*grass species* as fixed effects.

dominants, which leads to dramatically improved "whole plant" quality indices. In fact, we found that *Themeda triandra*, had lower quality indices for both CP and ADF when measured at both the plant part and whole plant scales, with very little differences in burned and unburned sites. Other studies have also found lower quality indices for *T. triandra* in burned sites relative to its co-dominant species (Okello 2002).

In unburned sites, it is more likely that *T. triandra* is "palatable" to grazers due to its structural morphology. *T. triandra*, particularly in unburned sites, has a low percentage of stem material and forms dense bunches of leaves close to the ground, enabling grazers to efficiently

capture high quality bites. In burned sites, we noticed that *T. triandra* quickly elongates stem tissue with prolific flowering (perhaps explaining its low CP stem values), which would make it more difficult for grazers to consume. For the *Pennisetum* species, the opposite pattern is present: in unburned areas they are structurally difficult to consume with high percentages of elongated tough, stem and in burned areas formed short, leafy mats of easily consumed forage.

LARGE HERBIVORE USE OF BURNED SITES

After counting more than 130,000 dung records over a two year period for a combined total of 300 km of dung transects, we included 10 grazers and/or mixed feeders in the study (Table 2), four of which are hindgut fermenters and six of which are foregut fermenters. We followed the lead of Cromsigt et al. (2006) in including warthog as a hindgut fermenter despite the fact they belong to the order Artiodactyla, all of which are foregut fermenters. Warthog (and all Suidae) are in many ways more similar to hindgut fermenters than foregut fermenters in that they (1) do not ruminate like the remaining foregut fermenters in our study, (2) have a relatively simple forestomach, and (3) possess a well-developed hindgut.

The study did not specifically quantify how cattle responded to burned sites, which would be an important topic of further research. Since cattle are tended by herders and moved across the landscape based on management decisions, their use of burn sites was not a true measure of their preferences. Moreover, we found it impossible to differentiate between buffalo and cattle dung and therefore these species were left out of the analysis.

	species	body weight	order	family	digestive gut type
Cana hara		(rg)	Lagomorpha	Loparidaa	ba
Cape hale	Lepus capensis	2	Lagomorpha	Lepondae	ng
impala	Aepyceros melampus	53	Artiodactyla	Bovidae	fg
Grant's	Cazalla granti	55	Artic de atula	Povidoo	fa
gazelle	Gazella granti	55	Aniouaciyia	Dovidae	ig
warthog	Phacochoerus	69	Artiodactyla	Suidae	hg*
	aethiopicus				
Jackson's	Alcelaphus	111	Artiodactula	Rovidae	fa
hartebeest	buselaphus jacksoni	144	Artiodactyla	Dovidae	iy
Beisa oryx	Oryx beisa	205	Artiodactyla	Bovidae	fg
Plains		075	Deriesedestule	F auridee	h a
zebra	Equus burcheili	215	Penssodaciyia	Equidae	ng
Defassa	Kobus ellipsiprymnus	200	Artiodootylo	Povidoo	fa
waterbuck	defassa	200	Aniouaciyia	Dovidae	ig
eland	Taurotragus oryx	475	Artiodactyla	Bovidae	fg
elephant	Loxodonta africana	3900	Proboscidea	Elephantidae	hg

Smaller bodied animals preferred burns more than larger bodied animals

We tabulated more than 130,000 individual dung records in the 18 different plots during the two-year period. Mean dung densities are displayed below separately for each species in burned areas, unburned areas within the plot, and neighboring unburned control transects (see Figure 3) for each of the burn patterns.





Figure 19. Mean dung densities (dung piles per 40 m^2) for each of the 10 species by treatment size (1, 9, and 81 hectares) and grain (*continuous* and *patchy*). Light grey indicates unburned patches within the treatment, white bars indicated dung in burned patches, and dark grey bars indicate mean dung in the neighboring control transects. Error bars are standard errors.

From these data we can highlight a few important points.

- Although it is problematic to infer relative population densities from dung densities, we can conclude, that in the absence of fire, Laikipia is dominated by larger bodied grazers, particularly zebra, which had the highest dung densities in unburned areas.
- Smaller bodied animals (hare, impala, Grants gazelle etc.) had the highest dung densities of all grazers in burned areas.
- The smaller the grazer's body size, the greater its preference for burned sites (as measured by a "burn/unburn" preference ratio).

We can look at these data in another way. If we calculate a burn preference ratio for each species by dividing the "mean dung in burned areas" by the "mean dung in burned areas + unburned areas", the effect of body size becomes readily apparent. We found a tight, negative relationship (Figure 20) between preference for burn sites and grazer body mass for both hindgut and foregut fermenters. In other words 90% of hare dung was found in burned sites, while only



Figure 20. Grazer preference for burned areas negatively scales to body mass for both (a) hindgut fermenters and (b) foregut fermenters. Mean preference indices (+/- SE) are from 18 burned plots where 'burn preference' is: dung in burned areas / dung in burned areas + dung in control transects. Regression equations on a log-log scale are: $y = 0.98x^{-0.14}$, $R^2 = 0.97$ and $y = 1.96x^{-0.22}$, $R^2 = 0.65$ and for hindgut and foregut grazers, respectively. The dashed horizontal lines indicate no preference or avoidance of burned areas.

30% of elephant dung was located in burned sites. The dotted lines indicate conditions where 50% of dung is in burned areas and 50% in unburned areas, suggesting no preference. It is interesting to note that zebra dung was found on average in equal amounts in burned areas and unburned areas. To the degree that dung densities are a good measure of grazing use, this suggests that zebra are not preferentially foraging in burned areas more than unburned areas.

Many landowners commented that one reason they are hesitant to burn is because of the way burned areas attract wildlife, particularly zebra, which may increase competition for grass with cattle. Our data raise some interesting new questions in this regard. Are zebra grazing more in burned areas than unburned areas, or are they simply resting in these areas to minimize predation risk? Perhaps zebra are only preferentially foraging in burned areas immediately after burning with the arrival of the rains, after which the burns are not preferentially grazed? Are zebra moving back and forth between burned and unburned areas to maximize both high quality and quantity of forage?

Future behavioral studies will be necessary to address the above questions. I began some of these observational studies in 2005 by sitting in a camouflaged blind to observe how animals were behaving in the burns. Zebras were frequently seen dust bathing, resting, and socially interacting, with very little time spent foraging. We can make limited conclusions from these observations because they occurred in a subset of the burns during the end of the rainy season.



Burn preference is related to grass quality (but depends on grazer body size)

While predator avoidance and other considerations undoubtedly contributed to the use of burned sites, our data suggest that smaller bodied animals preferred burned sites because of their dependence on the higher quality forage found in burned areas. Evidence for this is that grazer preference for burned sites was significantly related to variation in forage quality among burned areas. As grass matures its quality as forage declines (ADF increases), mainly due to plant cell wall thickening and declining leaf:stem ratios. As a result, the high spatial and temporal variability of rainfall in our study system created additional heterogeneity in forage quality and quantity between burned plots (Figure 6).

We found that smaller bodied grazers had higher preferences for the burned plots with extremely low ADF values (high quality), while the larger bodied species preferred burned sites with higher ADF levels (Figure 21), a pattern evident for both foregut and hindgut fermenters. CP values in the burned sites did not affect grazer burn preference regardless of body size (CP, p = 0.45; log body weight*CP, p = 0.23). We surmise that we did not find a high correlation between increasing plot CP and burn preference for smaller species because CP values in burned areas were not dramatically different than CP values in unburned areas. Additionally, the percentage of live leaf in the burned areas increased the burn preference index for small-bodied animals but not larger species.



Figure 21. Mean burn preference indices (+/- SE) for the ten grazers in the study as a function of changes in the acid detergent fiber (ADF) of grass clippings taken from <u>burned</u> areas in each plot. Smaller bodied animals demonstrate greater preferences for burned areas with higher quality forage (low ADF), while larger bodied animals preferred burned areas in which grass quality was low (high ADF).

Foregut fermenters preferred burns more then hindgut fermenters

Another piece of evidence supporting a forage quality explanation for why grazers used burned sites is that we found significant differences between how hindgut and foregut fermenters

responded to burns. After controlling for body mass, foregut fermenters had on average 78% of their dung in burned areas, while 54% of the dung of hindgut fermenters was found in burned areas. Also, the negative relationship between body mass and burn preference was steeper for foregut fermenters than hindgut fermenters (log body weight*gut, p < 0.0001).

Foregut fermenters are constrained to digest cellulose to smaller particle sizes in order to pass through their foregut, meaning they are more selective and dependent on higher quality forage than similar sized hindgut fermenters. In terms of how grazers might compete, this also implies that hindgut fermenters compete with foregut fermenters 3-4 times their body weight, which has been documented for zebra and buffalo. Pony (Equus caballus)

Body length: 164 cm



(Ovis aries) Body length: 110 cm



Figure 22. Representative gut anatomies for hindgut (pony) and foregut (sheep) fermenters showing the sites of cellulose fermentation. Hindgut fermenters have enlarged large intestines while foregut fermenters have compartmentalized stomachs. (Taken from Stevens & Hume 1998).
Total dung densities were highest in smaller sized burns

When all 10 grazer species were considered together, the smaller burns had overall higher dung densities. This pattern may result from a variety of mechanisms. Since smaller animals prefer burns more than larger animals, the smaller spatial scales may be perceived better by smaller animals. Higher grazer dung densities in smaller burns may also arise from the tendency for territorial males to mark these areas as preferred habitat with dung middens, which would be more difficult in large expanses of burned area. Lastly, if high quality forage is rare in an area (small burns comprise just a fraction of the landscape), the smaller burns may be areas of high competition among herbivores for forage.

Regardless of the behavioral mechanisms that gave rise to the pattern that the largest burn sizes (81 hectares) had lower overall dung densities, the lower dung densities in large burns translated into the



Figure 23. Total dung of all 10 species per sampling subplot (40 m²) averaged over treatment size (1, 9, and 81 hectares) and treatment grain (C = *continuous* burn, P = *patchy* burn). Error bars indicate standard errors.

grass in the larger burns growing back faster than in the smaller size classes.

Medium sized burns (9 hectares) persist as grazing lawns longer than larger and smaller burns

On average the 9-hectare burns were cropped closer to the ground by grazers than either the 1-hectare or 81-hectare burns. It is likely that the 1-hectare burns were small enough that they were overlooked by the larger bodied grazers and therefore grass growth more quickly returned to a taller height. In these burns the smallest grazers (hare and gazelle) were not able to keep the grass tightly cropped without the help of larger-bodied animals. The 9-hectare burns were cropped to a very short height (approximately 10 cm), persisting as grazing lawns for at least 1¹/₂ years after burning. Perhaps 9-hectare burns are at the right spatial scale to attract enough grazers to maintain the site as a grazing lawn, while the largest burn size (81 hectares) were less able to congregate grazers at sufficient densities to "keep up" with grass re-growth.



Figure 24. Mean grass heights in burned patches as a function of days since burning for 1 ha (open circles), 9 ha (grey squares), and 81 ha (filled triangles) burns. The heights for control transects were pooled from all of the control transects at each treatment (crosses). Photo was taken in a nine-hectare burn on Segera Ranch (SG9C04) more than 1 year after burning showing how grazers maintain the burn as a tightly cropped grazing lawn.

Smaller bodied animals preferred smaller burns

Ritchie and Olff (1999) have suggested that the coexistence of the multitude of large herbivore species in East African savannas is a result of their variation in body size. It is thought that smaller species are able to perceive the landscape at finer scales then larger species and thereby partition resources spatially. For example a 10-meter diameter patch of short grass may be perceived as a large grazing lawn to a hare, but is unnoticed by an elephant.

We predicted that the smallest burns would therefore be used the most by the smallest herbivores and the largest burns would be dominated by the largest herbivores, a pattern which is somewhat evident in Figure 25.



Figure 25. Percentage of total dung piles in burned patches grouped by body size classes for the three burn sizes and control plots. Data are means from 18 plots over the entire study period and patchy and continuous burns are combined. Means from 6 unburned control plots (2 at each size class) are indicated by "control plots". (*mega* = elephant, *large* = zebra, waterbuck, eland; *medium* = oryx and hartebeest, *small* = warthog, Grant's gazelle, and impala; *hare*=hare only.)

We found that burn patchiness had a greater affect on dung densities than burn size as displayed in Figure 26. When the treatments were combined to group burns with the same "pixel" or grain size, it is apparent that only the smallest bodied animals had high dung densities in treatments with small patch size (30 meters). As patch size increased, the larger-bodied animals were able to choose between burned and unburned areas in a way consistent with

predictions related to their preferences for high grass quality. For example, the largest species, elephant, was best able to avoid burns only at the largest grain size. The same concept is more easily viewed in Figure 27.



Figure 26. Mean "within-treatment" burn preferences as a function of body size for the 4 different patch sizes in the study. The schematic above the graphs indicates how treatments were aggregated for the analysis by pooling treatments based on treatment "grain" without considering total burn size (100 m patches combine the 1 ha continuous and 9 ha patchy treatments, 300 m patches combines the 9 ha continuous and 81 ha patchy treatments). Error bars are standard errors.

The largest factor that affects a grazer's use of burned areas is its body size, presumably because smaller body sizes dictate requirements for higher quality food. Larger bodied animals on the other hand, require high quantities of forage and can tolerate low quality, therefore they tend to avoid burns because of the low amount of grass in burned areas. If the size of the burn also affects how grazers respond to the burns, they we'd predict that small animals should have *high* burn preference ratios at *smaller* sized burns and large animals should have *low* burn preference ratios for *larger* sized burns. In other words, their decisions about spending time in burns should be maximized at spatial scales that match their body size, a pattern demonstrated in the graph below.



Figure 27. 'Within-treatment' preference indices as a function of average patch size for three representative grazers of varying body size, hare (squares), Grant's gazelle (circles), and elephant (triangles). Error bars are standard errors. Data come from pooling treatments based on treatment grain without considering total burn size. The circles indicate the relative patch size at which the species preference for burned areas

Do grazers coexist by selecting patch sizes and patch qualities that match their body size?

By merging an animal's preference for plant quality with this idea that smaller animals perceive patches at smaller scales than larger animals, we predicted that each grazer has a unique quality and patch size preference (as shown in Figure 28.) To assess this prediction we measured how the dung density of each grazer varied as a result of two variables, (a) the changes in plant quality, and (b) the size of the patch. For this analysis, we included both burned and unburned areas in just the *patchy* burns in order to determine if body size affected how animals perceived the landscape.



Theoretical prediction of body size effects on resource selection

Figure 28. Simplified diagram showing predicted resource partitioning among animals of varying body size based on their preferences along two axes, patch size and patch quality. Modified after the approach introduced by Ritchie and Olff (1999).

The graph below demonstrates that animals do seem to partition resources along both patch size and patch quality axes. Smaller bodied animals prefer smaller patches of higher quality, while larger animals prefer larger patches of lower quality. As emphasized earlier, high plant quality is necessary for smaller grazers, but this pattern also suggests that the <u>spatial</u> attributes of the plant quality affects grazer use. This offers support for the concept that savanna spatial heterogeneity of plant quality/quantity is important in promoting diversity of wild grazers.



Figure 29. Contour plots showing mean dung per 40 m² as a function of variation in grass quality and patch size. Data include dung counts from all burned and unburned patches from only *patchy* treatments (30 m patches means of three replicates of 1ha patchy, 100 m plots means of three replicates of 9 ha patchy, and 300 m plots from one replicate of 81 ha patchy). For each plot, at each patch size the dung density for each species was averaged at 50 g/m² intervals of dead leaf + stem biomass. Red areas are the lowest dung densities and blue areas the highest. The white boxes highlight the combination of plant quality and patch size where dung densities were the highest.

Fire effects on whistling thorn tree (Acacia drepanolobium)

Before burning we tagged more than 2000 individual trees and measured their stem diameter, the kinds of ants present, tree height, and extent of elephant browsing. After burning we re-surveyed all the trees and also noted if the tree was top-killed (all above-ground leaves/stems are dead but roots are still alive) or completely dead.

Fire disproportionately top-kills smaller diameter trees. Surprisingly, elephants preferentially forage on burned trees and prefer trees of larger diameter. Elephants frequently knocked down large burned trees in order to forage on leaves and twigs (Figure 30).

It is unclear why elephants seem to prefer burnt trees. It may be because the trees are not as vigorously defended by acacia dwelling ants. Nonetheless the combined effect of burning and elephant browse can dramatically decrease the density of *A. drepanolobium* many months after burning.



Figure 30. Elephant foraging on whistling thorn trees in a 1-ha patchy burn on Segera Ranch.

Figure 31. Fire top-kills whistling thorn trees of smaller diameter, while elephants preferentially browse larger trees, which have been burned. The combined effect is to increase overall tree mortality through time.

Disturbance and Bird Ecology in Laikipia, Kenya

A Report of the S.A.F.E Project and Related Research

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Introduction

Our project incorporated aspects of the Scale and Fire Ecology Project (S.A.F.E.) with research on recently-abandoned bomas to answer questions about the effects of traditional pastoralism on wildlife communities and the consequences of land-use change in the Laikipia District of Kenya. Traditional pastoralism in Laikipia combined anthropogenic fire with herding using bomas. Anthropogenic fire has been absent from this region since the 1950's, but cattle management has largely persisted using bomas, offering a rare opportunity to study the relative ecological impacts of both types of disturbances.

To date, most of the research on fire and grazing in Africa has centered on large mammals and ignored the consequences of altered disturbance regimes on birds. However, as important pest controllers, pollinators, seed-dispersers, and prey species for both humans and other animals (Watkinson and Ormerod 2001), birds deserve more attention. High levels of bird diversity generally coincide with high levels of diversity in other taxa; thus, birds can be useful in setting broader conservation priorities (Bennun 2000; Brooks and Thompson 2001). Understanding the responses of avian communities to landscape features and land uses will help inform and improve management practices in sub-Saharan African savanna ecosystems.

Specifically, we were interested in the following questions:

- How do the practices of controlled burning at different scales and livestock grazing using bomas affect avian abundance, diversity, and community composition?
- How do the effects of these disturbances compare?
- What are the possible mechanisms underlying these changes?

Background

Globally, savanna ecosystems are of particular conservation concern as they sustain large numbers of mammals, birds, and plants while supporting human communities and their associated land uses such as grazing by livestock. In Africa, two types of natural disturbances sustain savanna ecosystems: fire and grazing. These disturbance mechanisms have long been influenced by humans (Werner 1990; Roques et al. 2001). Maintaining disturbance dynamics in these systems is critical to biodiversity conservation.

East African savannas most likely exist in their present form because of a long history of frequent, anthropogenic perturbations. Ancestors of modern humans may have first begun burning the landscape on a large scale as early as 2.5 million years ago, thereby initiating a widespread conversion of tropical forest to grassland (Westbroek et al. 1993). Elemental carbon in marine sediments indicates that humans have dominated fire regimes in East African savannas for at least the last 10,000 years (Bird and Cali 1998). A second important anthropogenic disturbance arrived as early as 2500 BC (Diamond 1997) in the form of cattle, and pastoralists have dominated the region for the last 2000 years (Homewood and Rodgers 1991).

Traditional pastoralism in East Africa coupled grazing with controlled fire: Fire was used to remove rank vegetation, promote new growth, control woody shrubs, and control livestock parasites (Van de Vijver, Poot et al. 1999; Roques et al. 2001). In many areas, pastoralists further altered the landscape by clearing woody vegetation and building bomas, temporary thorn-scrub corrals, for their livestock. Once abandoned, the bomas and adjacent areas, now denuded and enriched with dung, became productive grazing lawns that persisted for decades (Stelfox 1986; Coughenour and Ellis 1993; Young, Patridge et al. 1995; Augustine 2003) and, along with fire, promoted landscape heterogeneity. Colonial land-use policies of the early twentieth century suppressed large-scale fire with potentially major consequences for biodiversity. In the absence of fire, bomas continue to serve as a major landscape modifier.

Methodology

Experimental Design

As part of the Scale and Fire Ecology (S.A.F.E) project, we tracked changes in bird abundance, diversity, and community composition on the 1, 9, and 81 hectare continuous burns to determine the role of a disturbance's scale in structuring avian communities. We did not

survey the patchy burns as part of this study. To assess the impact of traditional pastoralism on biodiversity, we compared the response of the bird community to controlled burns, recently-abandoned bomas, and undisturbed habitat. We compared the 9-hectare S.A.F.E. burns to a series of bomas that had been abandoned for less than 3 years. As bomas are continuously being established and abandoned, we were able to add plots over the course of the study. Five bomas were surveyed in 2005, six in 2006, and seven in 2007.

Sampling

Study sites were surveyed during February and March (1st dry season) just prior to burning in 2005 and in the subsequent 1st dry seasons in 2006 and 2007. We also surveyed the plots between June and August (2nd dry season) following the March through May rains from 2005 through 2007. We considered the two seasons separately since migration in and out of the system changes the character of the bird communities independent of the experiments.

To measure changes in avian abundance, species richness, and community composition, we employed the fixed-width transect method (Bibby 2000; Southwood and Henderson 2000). Two transects originated in the center of each plot and ran to the corners of the treatment at 90° angles to each other (Figures 1a and b). Two observers walked the length of the transect and recorded every bird sighted within 50m on either side. The treated portions of the transect were 100 m long on 1 ha burned plots, 200 m on bomas and 9 ha burns, and about 600 m on 81 ha burns. Surveys were conducted between 0630 and 1000 hours when birds were expected to be most active.



Figure 1a and b: Schematic of abandoned bomas (a) and 9 ha controlled burn plots (b). A thick dung layer characterizes the area inside the boma fence, and the impacted zone is largely treeless with short grass. Two transects (dashed lines), 100 m wide, start in the center of the plots and extend to the edge of the disturbance. The length of transects varied with the scale of the treatment.

Bird Community Response to Fires of Different Scales

February through March

In February through March of 2005, immediately after most of the sites were burned, the density (number of individuals per 100 m^2) of birds was highest on the 9 ha burned plots. Bird densities on the 1 and 81 ha plots did not differ significantly from pooled controls. During the drought of 2006, bird densities did not differ across sites (Figure 2). While we attempted to collect data in 2007, those results have been excluded due to incomplete sampling.

Trends in bird diversity across scales of disturbance mirror those seen in abundance. This is not surprising since encountering high densities of birds generally means observing a larger number of species. However, simple diversity measures that only consider the number of species on a site may mask important, but more nuanced patterns of species distribution.

In Figure 3, we present the percentage of observations of the most common species, those encountered at least 8 times, on each treatment as an indication of habitat use. In 2005, roughly half of the commonly observed species were found on burned plots and predominantly found on the 9 or 81 ha burns. In 2006, however, several species were observed more frequently on 81 ha plots.



Figure 2: The mean number of individual birds per 100 m2 \pm standard errors for 1, 9, and 81 ha burn plots during the first dry season (February through March) after burning and the same burned plots one year later are compared to undisturbed plots. Densities on 9 and 81 ha burned plots were higher than controls in 2005. The size of the squares corresponds to the size of the burned plots.

June through August

Figure 4 illustrates the dynamics of bird density from 2005 through 2007 during the months of June through August. While the trends were similar to those observed between February and March, bird densities on the 9 hectare burns were clearly much higher than any of the other treatments in 2005. After the onset of the drought, there were no clear differences in bird abundance between the different burn sizes or the controls.

As during February through March, a greater proportion of species were observed on burned plots relative to the undisturbed controls from June through August of 2005 (Figure 5). This preference breaks down in 2006 and 2007 with a higher proportion of birds observed on the 81 ha plots or the controls.

It should be noted that it is difficult to compare across sites of different sizes as sampling effort is typically greater on the larger sites. In this case, since we are presenting data pooled from all of the control plots, a larger proportion of the area surveyed was undisturbed habitat. Therefore, Figures 3 and 5 is biased in favor of undisturbed habitat meaning that burned habitats are potentially even more significant to most of the species than may appear on the figure.



Figure 4: The mean number of individual birds per $100 \text{ m}2 \pm \text{standard errors}$ for burn plots during the second dry season (June through August) after burning and the same burned plots one and two years later are compared to abandoned pastoralist corrals, or bomas, and undisturbed plots.



Percent Occurrence of the Most Common Species by Plot Size with Time: February through March

treatments: 1 hectare, 9 hectare, and 81 hectare, and pooled undisturbed control plots. During 2005 and 2006, most species show some preference for burned plots over controls, and some of those species were most often observed in the 9 ha plots. In 2006, there is movement by some species away from 9 ha burns to 81 ha plots, and the majority of species are more often observed on treated plots than controls. Data for 2007 is excluded due to incomplete sampling. Stars identify Palearctic migrants. Missing bars indicate species that were not observed often enough to be included Figure 3: Percent occurrence of species observed at least 8 times from February through March in 2005 compared to 2006 for the three burn



Percent Occurrence of the Most Common Species by Plot Size with Time: June through August

Time (Year)

treatments: 1 hectare, 9 hectare, and 81 hectare burns, and the pooled undisturbed control plots. During 2005 and 2007, most species show some preference movement by some species away from 9 ha burns to 81 ha plots, and a higher proportion of species are found primarily on controls. Missing bars indicate species that were not observed often enough to be included in the analysis. for burned plots over controls. During 2005, some of those species were most often observed in the 9 ha plots. During the drought year of 2006, there is Figure 5: Percent occurrence of species observed at least 8 times from February through March in 2005 compared to 2006 and 2007 for the 3 burn

Comparison of Burns and Bomas

While fire regimes have been severely altered across much of East Africa since European colonization, many managers have continued to manage their herds using bomas. We wanted to know whether abandoned bomas have been sufficient to maintain the landscape heterogeneity necessary for biodiversity preservation in the absence of fire.

February through March

In February through March of 2005, immediately after burning, bird densities were higher on both burned plots and bomas than undisturbed controls. In 2006, bird density dropped on the burned plots to the level of both bomas and controls. With the return of normal rainfall in 2007, bird densities on bomas appeared to increase, but the differences between treatments were not significant. The lack of significance in 2007 could be due to incomplete sampling due to weather (Figure 6).



Figure 6: The mean number of individual birds per $100 \text{ m}^2 \pm \text{standard errors}$ for burn plots during the first dry season (February through March) after burning and the same burned plots one and two years later are compared to abandoned pastoralist corrals, or bomas, and undisturbed plots.

Of the most common species observed from February through March in 2005, seven were predominantly found in burn sites (Figure 7). Of these, three were Palearctic migrants: Northern Wheatear (*Oenanthe oenanthe*), Pied Wheatear (*Oenanthe p. pleschanka*), and Barn Swallow (*Hirundo r. rustica*). During 2005, most species showed some preference for burned plots. In

2006, a greater proportion of species were observed on bomas; the majority of species were found on treated plots. In 2007, the majority of species were observed primarily on bomas although sampling effort was much reduced that year. Gaps in the figure indicate species that were no longer common after 2005. Significantly, one Palearctic migrant, Pied Wheatear, was observed almost exclusively in burned habitat over all three years. Of the other migrants, both Northern Wheatear and Barn Swallow declined in abundance by 2007.

June through August

In 2005, the density of birds on burned plots was significantly higher than both bomas and undisturbed controls. In 2006, after the drought, bird density on burns dropped to the level of controls. Densities on bomas did not change significantly from 2005 to 2006, and were higher than both the controls and the burned plots in 2006. With the return of normal rainfall in 2007, both burns and bomas were significantly higher than controls (Figure 8).

Of the most common species observed during 2005, some were predominantly found in burn sites, some predominantly in the undisturbed matrix, and others on both bomas and burns (Figure 9). During the drought of 2006, no birds were found predominantly on burns, and bomas feature more prominently. This pattern continued into 2007 where most of the species were found primarily on bomas or controls.



Figure 8: The mean number of individual birds per $100 \text{ m}^2 \pm \text{standard errors}$ for burn plots during the second dry season (June through August) after burning and the same burned plots one and two years later are compared to abandoned pastoralist corrals, or bomas, and undisturbed plots.



hectare burns, bomas, and undisturbed control plots. During 2005, most species show some preference for burned plots. In 2006, the majority of species are more often observed on treated plots than controls. In 2007, the majority of the observed species were observed primarily on bomas. Stars identify Figure 7: Percent occurrence of species observed at least 8 times from February through March in 2005 compared to 2006 and 2007 for all three habitats: 9 Palearctic migrants. Missing bars indicate species that were not observed often enough to be included in the analysis.

Mechanisms

The availability of food resources may be one of the primary mechanisms driving the observed patterns of bird abundance and community composition in the disturbed habitats. In August of 2005, I placed exclosures on 9 hectare burned plots, bomas, and controls to determine whether increased productivity on burned sites and old bomas translates into greater seed or arthropod production. There was little evidence that productivity in bomas translates into greater food resources, but cages inside burned areas had significantly more

the undisturbed habitat (Figure 10). Furthermore, when corrected for vegetation biomass, arthropod biomass is significantly higher in burned plots than controls (Figure 11). This is evidence that newly-burned areas are, in fact, highly productive and potentially provide greater food resources than undisturbed sites.

seedheads than cages in



Figure 10: Mean number of seedheads \pm standard errors in and out of grazing exclosures in and out of burned areas.



Figure 11: The mean ratio \pm standard errors of arthropod biomass to vegetation biomass from cages placed on 9 hectare burns and control plots. Arthropod biomass per gram of vegetation is significantly higher on burn plots than controls.

Percent Occurrence of the Most Common Species by Treatment with Time: June through August



Figure 9: Percent occurrence of species observed at least 8 times during the first summer after burning compared to the second summer after burning for all three habitats: 9 hectare burns, bomas, and 9 hectare undisturbed control plots. During the first summer after burning, most species show some preference for burned plots, but by the second summer, many are more often observed on bomas while others were not observed enough to be included in the analysis Over all three years, species are typically found more often on treated plots than in the undisturbed matrix.

Conclusions

Controlled fire and livestock grazing incorporating boma construction and abandonment, attract greater densities of birds and unique community assemblages when compared to the surrounding undisturbed matrix. Of the most common species observed during the study, the majority showed some preference for disturbed habitats. However, the effects of the disturbances vary with scale, season and time. While patterns of abundance and species richness were similar during the first and second dry seasons (February through March and June through August respectively) across years, there were significantly more birds from June through August.

Generally in 2005, when the burned patches were relatively fresh and rainfall was normal, most of the common species were primarily observed in burned areas, and burned plots hosted higher densities of birds than the undisturbed controls. Birds were particularly attracted to the 9 hectare burn plots which is consistent with existing research showing that bird community patterns are very sensitive to fine-scale habitat changes (Pons et al. 2003). In 2006 and 2007, however, the preference weakened, and a greater proportion of the common species were spending time in abandoned bomas. Those that continued to be observed on burned habitats were increasingly found on 81 hectare plots which may reflect a higher degree of habitat heterogeneity inherent in the larger burns. Alternatively, the larger area may be necessary to satisfy the foraging requirements of the birds under poor conditions.

In fact, drought conditions during 2006 equalized bird densities across treatments. Overall, yearly fluctuations were less pronounced on bomas than burns indicating that while fire may be important to birds in the short-term, bomas may exert a more lasting effect. Under conditions of poor rainfall, the quality of burned habitats, with their decreased vegetation cover, may be more likely to decline under such conditions. Bird densities on bomas, on the other hand, remained stable for all three years. Furthermore, bomas, with their combination of dung, scrub fence, and open grassy habitat, have greater internal heterogeneity than burned plots and controls. Abandoned bomas may provide refuge from drought to disturbance-loving species.

A particularly important characteristic of the burned plots from February through March is the presence of Palearctic migrants. Populations of Afro-Palearctic migrants have steadily declined over the past thirty years (Sanderson et al., 2006), so further alteration of fire regimes could have severe population consequences for the migrants that depend on burned habitat. One of the most striking results of this study is that very few species seem to be specializing in the undisturbed matrix habitat. The prevalence of undisturbed habitat may be a relatively recent phenomenon resulting from post-colonial human impacts on fire and grazing regimes. The small number of species specializing in undisturbed habitat illustrates the dynamic nature of savannas and the importance of disturbance to the maintenance of bird communities.

Overall, bomas have a longer-lasting effect on bird communities and should continue to be an integral part of management. However, while fires and bomas complement each other in terms of their impacts on bird communities, bomas are not substitutes for fires. The short-term but significant increases in bird abundance on burned plots signal potential population-level effects such as increased reproductive success (Bock and Jones 2004). Changes in management have driven declines in grassland bird populations worldwide (Powell 2006), so management that incorporates disturbance processes and promotes heterogeneity is essential (Bibby 2000).

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MANAGEMENT RECOMMENDATIONS

In July of 2006 the SAFE project sponsored a Fire Ecology Meeting at Mpala Research Centre in Laikipia, Kenya. The purpose of the meeting was to discuss with landowners the preliminary project findings and examine how fire may prove a useful tool in managing wildlife in Laikipia's rangelands. The meeting included more than 40 participants which included representatives



from: the Laikipia Wildlife Forum; Mpala, Jessel, Ol Pejeta, Borana, Kisima, and Lewa ranches; Mpala Research Centre; international researchers and students from multiple U.S. and U.K. universities; Moi University; University of Nairobi; and the Kenya Forestry Department. This written report serves to follow up that meeting with an overview detailing the completed project's findings.

Building on the participatory emphasis of this research project, landowners and conservationists were encouraged to consider ways in which burning might allow them to achieve multiple management goals. The following conclusions and management suggestions arise from the enthusiastic conversation at the 2006 meeting and subsequent completion of data analysis since that meeting, which is presented in this report.

1. Prescribed-burning can be used to create & maintain forage heterogeneity across the landscape, which should help perpetuate herbivore diversity.

Our project suggests that the amazing diversity of large herbivores, ranging in body size from hare to the elephant, is partly due to the natural variability in grass quality and quantity typical of savannas. Grass growing on black cotton soils is typically of very high biomass, but low quality. These kinds of habitats will favor large-bodied animals ("roughage feeders"), which may help explain the high population abundance of zebra and cattle in Laikipia. We suggest that introducing burning into the Laikipia region will enhance habitat for other wildlife, such as oryx, hartebeest, impala, and gazelle. These species require higher quality forage, which is available in burned areas. We, however, are not suggesting the use of burning to create grass quality improvements on the red, sandy soils. In these habitats, forage quantity does not become as abundant and grazing pressure can often maintain areas of shortly cropped high quality lawns independent of fire processes. All of the burn plots in our study were located on black cotton soils receiving rain between 500 - 600 mm annually. Fire-induced heterogeneity of grass swards is likely more important in these kinds of habitats where significant seasonal accumulation of grass biomass and declines in forage quality occur.

2. When using prescribed fires, consider burning smaller "focal" burns of intermediate size (10-25 ha).

The findings from the S.A.F.E. project emphasize the importance of paying explicit attention to the spatial scale of disturbances, which may facilitate achieving multiple management goals. If the management goal is to create grazing "hotspots" that provide habitat for small to intermediate sized animals, the use of smaller, focal burns (10-25 hectare) is recommended. By selecting smaller burn sizes, key foraging hotspots can be created for grazers while simultaneously reducing *Acacia* mortality, which serves as a key food resource for the growing black rhino and elephant populations. Intermediate sized burns are also likely to remain as hotspots of grazing activity longer than larger burns because they are preferred by smaller animals than larger burns. This may reduce the frequency with which a manager needs to burn. Smaller burns also preserve high biomass areas for cattle and/or larger herbivores, a potentially vital 'banking' effect where grass is saved in case of drought years. Focal burns have the added benefit of congregating animals in smaller areas where tourists can readily view them from selected roads and/or viewing areas, an important consideration for managers keen to develop ecotourism ventures.

3. Prescribed burning can reduce Whistling Thorn (*Acacia drepanolobium*) densities, particularly where elephant are present.

If the objective is to reduce whistling thorn, large burns are more useful because: (a) they burn hotter and therefore increase tree mortality, (b) they are more efficient in burning large numbers of trees, and (c) because of their large size, the grass will return to its pre-burn biomass more quickly than in smaller burns. Because elephant and rhino populations continue to rise in Laikipia, the effects of fire on whistling thorn mortality will likely be more pronounced as elephants seem to preferentially knock down and browse on trees which have been burned. We recommend using fire to open thickly bushed areas, but caution managers to monitor the density of whistling thorn in order to prevent removing too many trees. Smaller burns may be necessary to achieve multiple management goals.

4. While we did not explicitly measure the grazing behavior of cattle in burned sites, burning does enhance grass productivity, which may in part offset the increased competition that may occur between cattle and wildlife, which are attracted to burned areas.

Since cattle are herded by employees of the various ranches, their behavior does not accurately reflect their preference for burned areas. Being animals of large body size, their demands for forage quantity is high. However, the total live leaf biomass in burned areas is very similar to that in unburned areas, suggesting grazers have access to similar biomass of high quality forage. Since cattle are foregut fermenters with demands for higher quality forage relative to hindgut fermenters, they are likely to gain more in burned areas than similarly sized hindgut fermenters such as zebra. It is surprising to note that zebra, on average, had equivalent dung densities in both burned and unburned areas. In conversations with landowners regarding burning, many noted the large herds of congregating zebra in burned areas as evidence of increased competition between zebra and cattle. We observed this in the first survey after burning, a pattern that disappeared as the experiment proceeded. As noted previously, I personally observed zebra wallowing, dust-bathing, and grooming in burned sites, but rarely feeding. This may suggest that burning does not enhance competition with zebras as much as previously thought, but these observations deserve further study.

Conclusions

Developing a predictive model of how grazers respond to fire-induced heterogeneity is vital for conservation of wildlife species. While downward trends in wildlife numbers have occurred in many parts of Africa with multiple causes (Ottichilo et al. 2001), there is growing evidence that reduced sward heterogeneity due to fire suppression may differentially affect grazers of varying body size. Over the last 20 years, Thomson's gazelle, Grant's gazelle, and wildebeest have declined in the Ngorongoro Crater in Tanzania, while the bulk forage feeder, the

African buffalo, has increased (Estes et al. 2006). Estes et al. (2006) cited fire exclusion as one of the potential causes, which led to an increase in tall poor quality grass swards at the expense of the shorter, high quality forage needed by smaller grazers. Although similar scenarios have been suggested for Nairobi National Park in Kenya (Gichohi 1992) it remains to be tested whether using fire to create grass heterogeneity may mitigate wildlife declines in other parts of Africa.

Fire-induced vegetation heterogeneity may be an important component in the maintenance of large herbivore biodiversity and represents the fruitfulness of merging insights from body-size scaling, landscape ecology, and fire ecology. Our study highlights the important role that fire plays in promoting grazer coexistence and contributes to developing a predictive theory related to how faunal communities respond to fire, which has been lacking.

In areas where wildlife is restricted in movement (Laikipia and in fenced national parks) it is vital that we understand the scale related dynamics of heterogeneity. Heterogeneity, at multiple scales, may be a vital tool to facilitate the coexistence of wildlife with human communities. These findings have implications for how national parks are managed in East Africa and may help wardens and wildlife officials revisit their current policy of fire suppression.

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APPENDIX A: AERIAL PHOTOS OF SELECT BURNS



81-hectare patchy burn completed in 2004 on Segera Ranch. 4/9/2004



81-hectare continuous burn completed in 2005 on Jessel Ranch. 2/21/2005



9-hectare patchy burn completed in 2004 on Mpala Ranch. 4/9/2004



1-hectare continuous burn completed in 2004 on Segera Ranch. 4/9/2004



81-hectare continuous burn completed in 2005 on Segera Ranch. 2/21/2005



1-hectare patchy burn completed in 2005 on Segera Ranch. 2/21/2005



Nine hectare patchy burn completed in 2005 on Segera Ranch. 2/21/2005



Nine hectare patchy burn completed in 2005 on OI Pejeta Ranch. 2/21/2005
APPENDIX: B EQUIPMENT & FIRE SUPPRESSION

Implementing prescribed burning requires the ability to suppress and control fires safely. We designed a portable fire suppression trailer that was pulled by a landrover. We outfitted a landrover water tank with a Honda water pump and hose reel for use in wetlining. This allowed us to create fire-breaks around the perimeter of all burn patches.

Fire technicians were



equipped with Nomex fire retardant suits, fire helmets, goggles, and leather gloves. Portable back-pack sprayers were vital to controlling small spot fires and "mopping up", extinguishing smoldering stumps and dung piles after the fire is out. If you have questions or require assistance in designing your own fire suppression equipment, please contact Ryan Sensenig (rlsensenig@goshen.edu).



APPENDIX C: GRASS IDENTIFICATION GUIDE

> Pictorial Guide to the Common Grasses of the Black Cotton Ecosystem of Laikipia

> > **Compiled by Corinna Riginos**

Lintonia nutans

Common name(s): none known





Description: A perennial bunchgrass with short runners that can form many small tussocks. New leaves have a bluish color. Stem and leaf bases often flat.

Habitat: Damp soils and black clays

Use: Low grazing value



Pennisetum mezianum

Common name(s): bamboo grass



Description: Ascending perennial with hard, wiry stems, heavily branched, small leaves

Habitat: Open areas, damp soils and black clays

Use: Well grazed when young but becomes stemmy and unpalatable

Pennisetum stramineum

Common name(s): Maasai grass



Description: Ascending perennial with hard, wiry stems, heavily branched, long, slender leaves. Leaves sometimes reddish in color.

Habitat: Bushy areas, black clays, sometimes rocky sites. Dominates on termite mounds and older glades.

Use: Well grazed when young but becomes stemmy and unpalatable



Themeda triandra

Common name(s): red oat



Description: A perennial bunchgrass with characteristically red leaves in the dry season

Habitat: Open grassland and bushland on various soils

Use: A valuable grazing species, but palatability varies with soil and rainfall





Bracharia lachnantha

Common name(s): none known





Description: A dense perennial bunchgrass with broad leaves. New leaves have a bluish color. Stem and leave bases are round and silky-white.

Habitat: Damp soils and black clays

Use: A good grazing grass

