The effects of fire regimes on distribution and diurnal activity of African ungulates in Kruger National Park, South Africa

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Abstract

The effects of fire on herbivore distribution and behavior have important management implications when assessing habitat and nutritional qualities of herbivores. Many factors including top-down and bottom-up processes as well as biotic and abiotic factors influence ungulate selection of forage and habitat across a landscape. Although there has been much research on herbivore distribution in relation to fire and physical attributes of herbivores, only a small amount of research has been conducted assessing herbivore behavior across differing burn treatments. In this paper I aim to identify if: 1) grazers are found most often on annually burned plots or plots burned at longer frequencies, 2) the behavior of grazers differ across burn treatments, and 3) grazer diurnal activity is differentiated across burn treatments. Herbivore counts and behavioral surveys were collected on three different experimentally burned plot treatments in Kruger National Park, South Africa. As expected, herbivores were found most often on annually burned plots. However, grazing was observed most often on 3-year burn sites. Additionally, vigilance behavior was not statistically different in annually burned sites vs. 3-year burn sites. Further research needs to be conducted with larger sample sizes to assess the difference among smaller and larger bodied species, seasonality effects, and a broader range of fire frequencies.

Introduction

The roles top-down and bottom-up trophic forces play in natural communities have long been a source of heated debate among ecologists.[1] Selective foraging by herbivores, in response to plant nutrient quality or predation, can alter how an ecological community will be organized.[1] A bottom-up hypothesis to explain herbivore habitat preferences suggests forage is the deciding factor for habitat selection. Whereas a top-down hypothesis states predators, or other higher factors, are the deciding factors for habitat selection. Therefore it is highly important to understand top-down and bottom-up interactions to explain and comprehend the many complicated interactions that occur in the natural environment.[2]

A variety of factors, biotic and abiotic, contribute to foraging selection of ungulates across the landscape. Biotic factors include resource availability[3] and competition,[4] food preferences[5] and the risk of predation while foraging;[3] whereas external abiotic factors such as fire and rainfall are also important in shaping distribution of ungulates across a landscape.[6,7] In addition, physical aspects of an ungulate are also highly important in shaping distribution of herbivores. Attributes such as stomach type and body size are both highly important when assessing distribution of ungulates. External factors such as rainfall and predation, as well as physical variation such as body size and stomach type, do play a crucial role in the ecology of habitat and habitat selection in most African savannas. Therefore, Kruger National Park in South Africa provides an ideal system for studying ungulate behavior in relation to fire regimes.

Among grazers in the African ecosystem, it is believed the distribution and behavior of smaller-bodied species are limited by predation risk, whereas populations of larger-bodied species are limited by forage availability.[8,9] Furthermore, larger-bodied species generally prefer areas of low tree density (such as annually burned areas) possibly because of greater nutrient quality.[8] For example, an African elephant may choose an annually burned plot to gain the best nutrient quality available in a given set of time. The elephant, therefore, is choosing a plot that holds the highest daily intake and thus can eat less food in a given amount of time but obtain a higher energy value than it could in another plot with plants exhibiting lower nutrient quality (such as a plot burned every three years). Smaller-bodied species are more susceptible to predation and exhibit higher amount of predator vigilance which is why smaller-bodied species are thought to choose annually burned plots. A Steenbok, a small-bodied ungulate, for example, has a variety of predators due to its small size. Because of this the Steenbok should choose annually burned plots to forage in most often because it has a better chance of detecting a predator in a habitat with a low amount of trees and shrubs (as is exemplified in annually burned plots). Therefore, small-bodied individuals will choose annual burns for vigilance reasons and large-bodied ungulates will prefer annually burned areas for nutritious reasons.

Savanna ungulates are a big factor in driving habitat selection and facilitating species coexistence.[10] In general, animals are attracted to burned areas due to the new growth and rich nutrients found in burned plots.[6,7,11,12] High grass cover (and therefore greater biomass) and greater abundance of trees and shrubs are typical of tri-annually burned and unburned plots, whereas low grass cover is typical of annually burned areas.[13,14] In a top-down trophic cascade hypothesis a tri-annually burned and unburned plot would be riskier for ungulates because of higher vegetation obstruction due to increased amounts of shrubs and trees present thus creating a lower visibility of predators.

Another important factor known to influence ungulate distribution on a landscape is the idea that grazers should select patches for the highest daily nutrient intake and highest daily digestible intake. This may differ among ruminating herbivores and non-ruminating herbivores.[10,12,15] Ruminants (foregut fermentors) tend to forage in both burned and unburned areas as they are able to better digest low nutrient forage due to fermenting cells in their digestive tract.[10,15] Non-ruminants (hindgut fermentors) on the other hand are restricted to high-quality forage, such as those found on annually burned plots, as they are constrained by the rate that forage passes through their digestive tract.[12] Therefore, non-ruminants should be observed most often on annually burned plots whereas ruminants should be found equally on all plots. Thus, ruminants are more widely and evenly distributed across the landscape than non-ruminants due to their betteradapted digestive tracts.[10]

The African savannah has a large array of species. Therefore, it is also important to consider how body size affects nutrient and digestible intake. Generally speaking, smaller bodied herbivore species require higher quality food than larger species due to their higher metabolic demands, while larger bodied species require greater quantities and are more tolerant of lower quality food.[7] Thus, smaller bodied herbivores tend to be non-ruminants whereas larger bodied herbivores tend to be ruminants. Within ruminant types, smaller bodied herbivores should prefer burned areas more than larger bodied herbivores because there is higher nutrient quality in these areas.[7,16] This also exemplifies the fact that smaller bodied animals require less total energy, but more energy per unit of body mass or area of the landscape.[7]

Lastly, it is important to consider the diurnal effects on herbivores. Ecology of fear research has found that rock hyraxes (*Procavia capensis*) have higher giving up densities (GUD) during the early morning and late afternoon periods of the day.[17] This may suggest a marginal value of energy driving foraging or higher predation risks from ariel predators. In conjunction with the previous study, research in klipspringers (*Oreotragus oreotragus*) exemplified the lowest GUD levels during the middle of the day, and thus high GUD levels in the morning and evening.[18] This again could be due to perceived predation risk as predators spend the hottest parts of the day (the middle of the day) sleeping and saving energy, and hunt/move most often during the coolest parts of the day: generally between dusk and dawn. Thus, both smaller and larger-bodied species have higher GUD levels during the morning and evening.

Although there has been much research done looking at herbivore distribution in relation to fire as well as herbivore distribution across a landscape in relation to physical attributes of herbivores, little research has assessed herbivore behavior across different burn treatments. In this paper I aim to identify if: 1) grazers prefer annually burned plots over plots burned at longer frequencies, 2) if behavior of grazers differs across burn treatments, and 3) grazer diurnal activity is different between burn treatments.

Hypotheses

1. *Grazers will be found most often on annually burned plots rather than those burned at longer frequencies.* Grazers should choose a plot according to the highest nutrient intake available. Thus, grazers should choose an annually burned plot over those burned at longer frequencies due to the higher nutrient quality of plants exhibited in annually burned areas.

2. *Grazer diurnal activity will differentiate according to time of day.* Grazer diurnal activity should differentiate according to time of day due to the fact that grazers should be more vigilant in the early morning and evening when predators are present. Additionally, herbivores should be observed grazing more often during the early morning and evening due to the high temperatures and energy expenditure in the hottest part of the day.

3. *Grazer behavior and diurnal activity will differentiate across burn treatments.* Grazers should choose annually burned plots due to the high nutritional quality of forage found in these plots. Therefore, grazing behavior should be depicted most often on annually burned plots. Additionally, herbivores should exemplify lower amounts of vigilance in annually burned plots in comparison to plots burned at longer frequencies due to higher visibility in annually burned plots.

Materials and methods

Study site

With nearly two million hectares of land (covering approximately 7,332 square miles), Kruger National Park is the largest park in South Africa. Kruger National Park makes up part of the Great Limpopo Transfrontier Park in the north eastern portion of the country. This "peace park" links with Gonarezhou National Park in Zimbabwe and Limpopo National Park in Mozambique allowing animals to roam freely throughout their habitat.

Kruger National Park is in a subtropical climate with hot humid temperatures in the summer reaching at or above 38 °C (100 °F). There are two distinct seasons in South Africa: the rainy season, extending from September until May, and the dry season, extending from June through August. This study was conducted during the rainy season from January to March.

The park encompasses many different vegetative habitats including Baobab sandveld, Mopane scrub, Lembombo knobthorn-marula bushveld, mixed acacia thicket, Combretum-silver clusterleaf woodland on granite, and riverine forest.

My study sites were located in Satara Rest Camp in the east central portion of the park. Savannah grazing land is dominant in this region of the park. Grass species such as *Themeda triandra, Panicum sp.*, and *Bothriocloa sp.* dominate much of the grasslands. *Acacia sp., Sclerocarya caffra* (marula trees), and *Colophospemum mopane* were the dominant tree species in the area. These central grasslands contain the highest lion population in Kruger National Park. This nutritious grassland also supports some of the largest herds of grazers including plains zebra (*Equus quagga*), cape buffalo (*Syncerus caffer caffer*), common impala (*Aepyceros melampus melampus*), giraffe (*Giraffa camelopardalis*), blue wildebeest (*Connochaetes taurinus*), and African elephant (*Loxodonta africana*). Multiple predators including lion (*Panthera leo*), leopard (*Panthera pardus*), cheetah (*Acinonyx jubatus*), African wild dog (*Lycaon pictus*), and spotted hyena (*Crocuta crocuta*) also dominate the landscape.

Three differing sites were analyzed in the surrounding vicinity of Satara Rest Camp: Satara, N'wanetsi, and Marheya. Additionally, three experimental burned plot treatments at each site were surveyed: an annual controlled burn, a tri-annual controlled burn, and a 20-year controlled burn serving as a control. Each of the nine experimentally burned plot treatments were subjected to free ranging grazers.

Field procedures

Herbivore counts

Herbivore counts were done a minimum of two days a week on each burn site. Counts were done from a vehicle; the vehicle was driven in one direction around the burn plot, each of which varied in length. However, the mean plot was approximately 1 km^2. Counts were done at four time intervals: 6 am to 9 am, 9 am to 12 pm, 12 pm to 3 pm, and 3 pm to 6 pm. Each burn plot was counted for herbivores at each time interval at least once a week.

Herbivores were only counted when inside or foraging on the boundaries of the burn plot. Herbivores were not counted when passing through the plot or when entering the plot when a count was in progress. Counts were variable in length but lasted anywhere from 10 minutes to 1 hour depending on how many behavioral surveys needed to be conducted. Herbivores species were identified and counts were recorded for each species. Weather was observed and recorded to identify outlying days or occurrences in these data. Otherwise, weather was considered a non-factor variable for the purposes of this study.

Herbivore behavioral surveys

Behavioral surveys were done in conjunction with herbivore counts when herbivores were available. Species were counted and separated into categories based on sex, age, and separated by species and group size. Group size was separated into four categories: lone forager (one herbivore), a pair of foragers (two herbivores), a small group of foragers (three to six herbivores), and large groups of foragers (more then six herbivores). Group size was estimated when 20+ animals were available. When a group contained juveniles, herbivore behavioral surveys were randomly assigned to capture the appropriate proportion of individuals with and without offspring. Female individuals closest to juveniles were considered to be the parent of the juvenile.

Individual behavioral surveys were taken on approximately 30% of the individuals available. Each individual was observed for five minutes and behaviors were recorded every five seconds throughout the period. Eleven behaviors were exhibited on plots including: browsing, foraging, grazing, grooming, laying, moving, ruminating, vigilance, socializing, standing, and time spent out of sight. Browsing was recorded when an herbivore was observed eating shrubs. Grazing was recorded when an herbivore was observed eating grass. Foraging was recorded when an herbivore was eating but whose view was obstructed by habitat structures. Grooming was recorded when an herbivore was grooming itself. Laying was categorized when an herbivore was resting but not ruminating. Moving was categorized when an herbivore moved two or more steps in a particular direction. Ruminating was categorized when an herbivore was seen regurgitating its food and re-chewing. Vigilance (scanning) was recorded when an animal raised its head and looked around before continuing to eat or when the animal or group of animals would rapidly exit the area from an effect unknown to the observer. Socializing was categorized when an herbivore was playing or grooming another individual. Standing was categorized when an individual was standing but not ruminating. Time spent out of sight was categorized when an herbivore was standing behind obstructing vegetation or if it moved outside of the plot while the survey was in progress.

Data analysis

All data was compiled in an Microsoft Excel spreadsheet and categorized based on species, plot, and the four time periods mentioned previously in the field procedures section. Elephants and giraffes were not included in the data set because of lack of observations permitted in the time period. Therefore, only zebra, impala, and wildebeest counts and behavioral surveys were analyzed. The control plots were only included in the distribution data analysis, as only two animals were identified in these plots during my study. Therefore not enough data was present to exhibit differences in behavioral or diurnal patterns of grazers in control plots. Additionally, not enough data was collected to test the difference between body size or ruminating and non-ruminating herbivores; therefore all herbivores were grouped into one category.

The first hypothesis – grazers are equally distributed across burn plots – was tested by computing a chi-squared test ($\alpha=0.05$) in Microsoft Excel.

The second hypothesis – grazers behavior will be equally exhibited across burn treatments – was tested by computing a chi-squared test ($\alpha=0.05$) in Microsoft Excel. The top six behaviors exhibited were chosen for analysis: grazing, standing, moving, ruminating, vigilance, and browsing. Each behavior was re-quantified in order to get a total of all behaviors equal to 100%. Behaviors were then categorized based on time of day: early morning (6 am-9 am), mid-morning (9 am-12 pm), early afternoon (12 pm-3 pm), and evening (3 pm-6 pm). Furthermore, diurnal activity was then categorized based on distribution: early morning on annual burns, evening on annual burns, early morning on 3-year burns, and evening on 3-year burns. There was not a significant amount of data for the mid-morning or early afternoon periods for 3-year burns and, therefore, this data was excluded from the analysis of distribution in conjunction with diurnal activity.

Additionally, paired comparisons for the proportion of time spent in each of the top six behaviors for each individual in a five minute period were made for: early morning versus mid-morning, early morning versus early afternoon, and early morning versus evening foraging behavior using a two-sample, one-tailed t-test assuming equal variances in Microsoft Excel. A Bonferroni correction was then implemented to gain an alpha value equal to 0.017. The Bonferroni correction was used to counteract the multiple comparisons from the three t-tests mentioned above.

The third hypothesis – grazer diurnal activity will be equal across burn treatments – was analyzed using a chi squared test ($\alpha=0.05$) in Microsoft Excel. Additionally, foraging and vigilance behavior in relation to distribution was analyzed using a Two-Factor Weighted ANOVA with Unequal Sample Sizes in Program R ($\alpha=0.05$).

Results

Hypothesis 1

As expected, herbivores were more prevalent on annually burned plots then control plots ($p=0.00001$) (Figure 1). Twenty-seven grazers were observed in the annually burned plots, thirteen in the 3-year burned plots, and two in the control plots. No precision estimates were taken on these results, as data was not modified.

Hypothesis 2

As expected, diurnal activity was highly variable depending on time of day (Figure 2). Grazing and browsing behavior combined was higher in the evening ($p=0.02$) (Figure 3). Grazing was most pronounced in the early morning (SE=29.35), mid-morning (SE=18.80), and evening (SE=33.3). Differences in grazing activity during the early vs. mid-morning ($p=0.28$) and early morning vs. early afternoon ($p=0.27$) were not statistically significant. As shown in Figure 3, grazing behavior was observed more often in the evening than in the early morning ($p=0.046$). However, the behavior of grazing in the evening (SE=33.3) had a larger standard error then in the early morning (SE=29.35) meaning this behavior could have been less variable during both the early morning and evening times then what the data presents.

Standing was portrayed more often during the mid-morning (SE=18.80) and early-afternoon (SE=12.91) as expected due to the high temperatures during this time and the low amounts of energy needed to stand. Interestingly, ruminating was only seen during the early (SE=24.97) and mid-morning time intervals (SE=22.62). This may be due to the fact that animals are digesting their food after the previous evening and early morning intake. Browsing was not portrayed during the early morning period and is highest during the evening (SE=26.93). Additionally, vigilance spiked during the early morning (SE=8.13) and evening (SE=5.40).

Hypothesis 3

As hypothesized, herbivore distribution and diurnal activity vary according to burn treatment (Figure 3). Opposite from what was hypothesized, herbivores were shown more often to graze in 3-year burn plots then annually burned plots ($p=0.017$ and $p=0.033$ respectively). Standard error was much higher during the evening then in the early morning: signifying that behaviors in the evening are more variable compared to those in the early-morning (Table 1). However, time was not a significant factor in

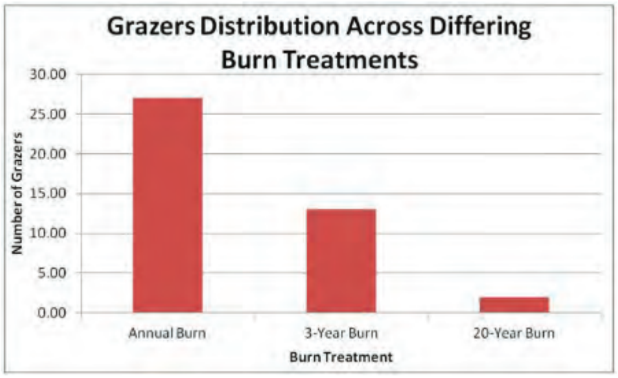

Figure 1: Grazer distribution across three burn treatments: annual burn, 3-year burn, and a 20-year burn serving as a control.

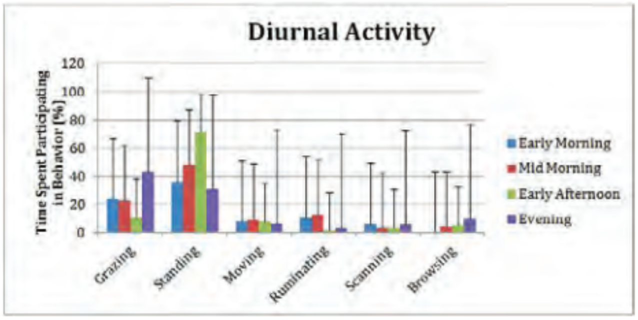

Figure 2: Diurnal Herbivore Activity with positive standard deviation bars.

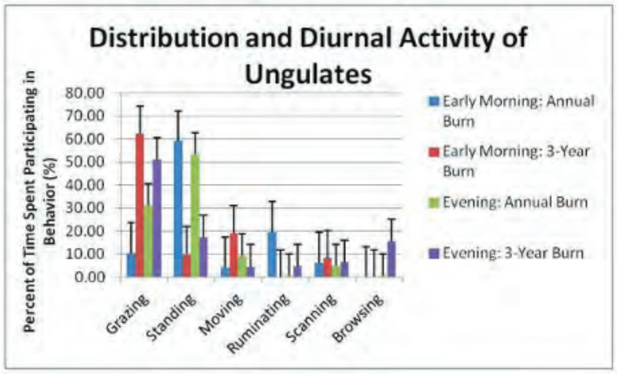

Figure 3: Distribution and diurnal activity during the early morning and the evening with positive standard deviation bars.

	Early Morning		Evening	
	Annual Burn	**3 Year Burn**	**Annual Burn**	**3 Year Burn**
Grazing	**16.15**	**26.79**	**32.27**	**33.55**
Vigilance	**9.86**	**4.16**	**5.91**	**5.32**

Table 1: Distribution and diurnal activity standard errors in percent for grazing and vigilance behaviors.

foraging behavior on annually burned plots versus 3-year burned plots (p=0.46 and p=0.16 respectively). Also opposite of what was expected, vigilance behavior was not statistically different in plots burned every three years versus plots burned annually (p=0.55) (Table 1).

Discussion

My results showed more herbivores on annually burned plots, which was in conjunction with additional studies stating that grazers are more often attracted to annually burned plots.[11,12,19] However, herbivores were observed to graze most often on 3-year burn plots, which may indicate that annually burned plots may not have higher nutrient quality than 3-year burn plots, as previously thought.

Diurnal activity was highly variable depending on the time of day. Generally, grazing was exhibited most often during the evening which was different from my original hypothesis that grazing would be most prevalent in the early morning and the evening. This would be an accurate analysis as the middle portions of the day are generally much warmer than the early and late portions of the day. Previous studies have also found higher giving up densities during the middle portions of the day for klipspringers and rock hyraxes.[17,18] Because ungulates tended to forage in the early and late parts of the day, it would make sense that standing would be the key behavior exemplified during the middle of the day as it consumes less energy than grazing. Interestingly, ruminating was almost only seen during the early and mid-morning time intervals. This may be due to the fact that animals are digesting their food after the previous evening intake as well as the early morning intake.

Distribution and diurnal activity also varied across burn treatments. Herbivores grazed more often in 3-year burn plots than annually burned plots. This is different from previous research suggesting that ungulates may choose annually burned plots for nutritional quality.[11,12,19] Therefore ungulates may choose 3-year burn plots during feeding times for higher nutrient quality. Herbivores may spend the majority of their time grazing in 3-year burn plots in the early morning and evening and then switch to annually burned plots during the hottest parts of the day in order to assess predators' presence more readily. Additional research needs to be conducted to test this hypothesis. Opposite of what was hypothesized, vigilance was indifferent in annually burned plots versus plots burned every three years. This may show that there are additional variables attracting herbivores to annually burned plots over 3-year burned plots. Further research needs to be conducted assessing this statement.

Management implications and conclusion

It is extremely important to incorporate human induced disturbances into conservation plans and diversity patterns.[19] The effects of fire on herbivore distribution and behavior are important for assessing habitat and nutritional qualities of herbivores. For example, the act of burning areas has been useful for managing habitats of two competing species. If there is a specific overgrazed habitat, a manager or farmer may be able to burn a nearby field allowing for re-growth in the overgrazed area. My study supports previous research that has observed that burning an area can increase ungulate use by up to twelve times.[10]

Additionally, competition between two species with overlapping habitats could be mediated through controlled burns. In the United States, black-tailed prairie dog colonies are often overgrazed by bison in areas where the two species overlap. A partial solution is to burn an area nearby for bison to graze which reduces the use of the bison colony by 30-60%.[10,20] Thus, controlled burns have been an effective method for mitigating the impact on two conflicting species.[21]

In a large park such as Kruger National Park, there are many competing and overlapping species especially amongst the ungulates. In the Satara area alone there are six different species of ungulates. Therefore, controlled burns are a good mitigation technique to reduce competition between these ungulates. Additionally, by having different fire frequencies, a park manager allows for the highest variety of habitat in a given area, thus also allowing for high species diversity. In order to allow for the maximum amount of biodiversity in Kruger National Park, the best way is to allow multiple habitats exhibiting different fire intervals throughout the park. As this is already being done in Kruger National Park, my recommendation is that it is continued for the overall health and well being of biodiversity of the park.

With higher diversity one may infer a larger risk of competition in the area. However, with many varying burn plots each species will congregate towards plots that will yield the highest potential for the sustenance of its own life. In other words, having a variety of habitats allows for animals to expand across a landscape to decrease the amount of competition in an area.

Burning is also of importance during seasonality shifts when grasses die and ungulates are forced to feed on trees and shrubs. It is then highly important for managers to have a good balance of annually burned plots and plots burned at longer fire frequencies. This allows for animals to graze on high quality plots (such as annually burned plots) in the summer months after the rainy season and plots burned at longer fire frequencies exhibiting higher amounts of shrubs and trees in the winter months.

Future studies should be conducted to further assess impacts of fire on herbivore behavior and distribution in relation to body size differences, seasonality effects, and fire frequencies to expand upon the highest potential for any given land.

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