

Habitat selection by large herbivores in a southern African savanna: the relative roles of bottom-up and top-down forces

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Abstract. Animals must often balance food availability and predation risk when selecting habitat. Here, we examined habitat preferences of large mammalian herbivores in a long-term fire experiment in the Kruger National Park, South Africa to assess the role of bottom-up (e.g., forage quantity/quality) and top-down (e.g., predation risk) processes in driving herbivore distributions. We focused on experimental plots (~10 ha on average) that have been burned in the winter (August) since 1954 at 1- and 3-yr intervals, or left unburned ($n = 3$ per burn type). Herbivore distributions (during both day and night) and plant community structure were surveyed on each plot during the growing seasons (November–March) of 2005–2006, 2006–2007, and 2007–2008. Overall, we sighted 4,187 individuals representing twelve species of mammalian herbivores. Impala (*Aepyceros melampus*), zebra (*Equus quagga*), and wildebeest (*Connochaetes taurinus*) comprised 37%, 28%, and 18% of all individuals observed, respectively. Several species such as African buffalo (*Syncerus caffer*), wildebeest, and giraffe (*Giraffa camelopardalis*) exhibited a significant trade-off between food acquisition and minimizing predation risk by foraging in areas with lower density of woody vegetation. We also observed significant day vs. night dynamics in herbivore habitat selection. For example, zebra utilized annual or triennial burns during the day depending on which years the plots were burned, but they avoided triennial burns with dense woody vegetation in favor of more open annual burns at night when predators such as lions (*Panthera leo*) are more active. Similarly, the smaller, mixed-feeding impala appeared to use riskier habitats with more diverse forage options during the day (triennial burns and unburned plots) but used less risky habitats at night (annual and triennial burns). Diurnal vs. nocturnal patterns are often overlooked in studies of habitat selection but are necessary for understanding the factors that shape distribution. The variation we observed in herbivore distribution patterns during this three-year period indicates that different species exhibit different trade-offs with respect to food and predation risk. Factors such as body size, nutritional requirements, prey escape tactics, and recent fire history likely mediated these interspecific differences.

Key words: body size; grazing; herbivory; Kruger National Park; optimal foraging; predator-prey; resource selection function; South Africa; ungulate.

INTRODUCTION

Both food availability and predation risk contribute towards driving patterns of habitat use in animals (Fryxell 1991, Brown and Kotler 2004). In African savannas, ungulates often track resource availability over time and space in order to maximize their nutrient or forage intake or to maintain access to water (Fryxell and Sinclair 1988, McNaughton 1990, Fryxell et al. 2004, Winnie et al. 2008, Chamaille-Jammes et al. 2013). However, variation in predation risk among habitats may complicate the decision to forage in the most rewarding habitats. Many African savannas support a diverse suite of large predators (e.g., lion, leopard, cheetah, wild dog, and spotted hyena) that prey on ungulates and can have a substantial impact on prey populations (Funston and Mills 2006, Owen-Smith and Mills 2008). Evidence from ungulate-predator systems across several terrestrial habitats has also shown that prey species avoid areas frequented by predators or have higher perceived risk of predation (Creel et al. 2005, Ripple and Beschta 2006, Riginos and Grace 2008, Valeix et al. 2009). If valuable foraging areas and areas of high predator use or predation risk often overlap, ungulates must balance obtaining the resources they need to survive while avoiding predation.

In African savannas, fire frequency often influences many of the factors impacting ungulate distribution, including both forage quality and predation risk. For example, recently burned areas quickly flush new, tender grass shoots, which attract herbivores to the easily digestible forage (Archibald and Bond 2004, Sensenig et al. 2010). Yet, continued frequent fires may also significantly decrease soil nutrients and plant forage quality (Blair 1997, Anderson et al. 2007). In contrast, infrequently burned savannas often have high soil nitrogen and palatable and nutrient-rich grass species that should also attract herbivores (Treydte et al. 2008). However, decreasing fire frequency increases vegetation cover

and tree density, providing more cover for predators (Hopcraft et al. 2005) and decreasing visibility and the subsequent ability of herbivores to detect and escape from predators (Funston et al. 2001, Riginos and Grace 2008). Consequently, herbivores may avoid areas with relatively taller herbaceous vegetation or denser woody cover (Mills and Fey 2005, Riginos and Grace 2008) or spend more time being vigilant in these areas rather than feeding (Smith and Cain 2009, Pays et al. 2012). Thus, foraging among areas of savanna with different fire return intervals may represent a trade-off between acquiring quality forage and avoiding predators.

Because the suite of herbivores in African savannas varies considerably in body size, metabolism, foraging mode, anti-predator tactics, and water dependence, among other traits (Owen-Smith 1988, du Toit and Owen-Smith 1989, Illius and Gordon 1992), the forces that shape herbivore distribution are likely to vary considerably across species (Bell 1971). For example, the high metabolisms of smaller ungulates such as impala necessitate that these herbivores favor high quality forage with a minimal long-term tolerance for the low quality foods that larger herbivores with slower metabolisms can survive on (du Toit and Owen-Smith 1989). As a consequence, the distribution of smaller herbivores may be more highly influenced by forage quality than that of larger herbivores. Yet, smaller herbivores often face a higher predation risk (Sinclair et al. 2003, Radloff and du Toit 2004, Owen-Smith and Mills 2008), possibly making it more likely that they will avoid areas with low visibility and increased probability of predator encounter. Thus, interactions among biotic and abiotic forces that shape prey distribution and behavior will vary across species depending on their natural history (Wirsing et al. 2010).

In this study, we examined patterns of herbivore distribution in a fire-managed savanna to determine how bottom-up and top-down forces

shape interspecific differences in habitat selection. Our study site in the Kruger National Park, South Africa has a long history of successful fire management (van Wilgen et al. 2000) and a herbivore and predator assemblage typical of many existing protected savannas in southern Africa (du Toit 2003). We quantified herbivore distribution patterns via visual diurnal and nocturnal surveys and via dung transects over three years in areas of savanna experiencing different fire return intervals. We also characterized the habitat (e.g., plant community structure, plant nutrient content, soil nutrient content) across the different fire regimes. In addition, we characterized the vegetation surrounding sites of kills by lions, the dominant predator in the region, of the most common prey herbivore species. With these data, we were able to evaluate the following main predictions:

1. Grazing herbivores would preferentially use plots that were recently burned because these areas had either greater quantity or quality of grasses.
2. Browsing and mixed-feeding herbivores would select for infrequently burned plots with higher cover of forbs and woody vegetation.
3. Lion kills of smaller-bodied, more vulnerable species would be in areas of taller grass and denser woody vegetation (e.g., higher risk).
4. Smaller, more predation prone herbivore species would avoid areas that are likely more risky (e.g., areas with denser vegetation) while larger-bodied species would show little influence of vegetation structure on distribution.
5. Herbivores would select for less risky sites at a higher proportion at night when predators are actively hunting.

MATERIALS AND METHODS

Study site

Kruger National Park (KNP), South Africa (22°25' to 25°32' S, 30°50' to 32°2' E), which encompasses nearly 2 million ha, has a long fire history that is currently a combination of prescribed management and natural fires (van Wilgen et al. 2000). These fires result in a mosaic

landscape, with fire frequencies in a given region ranging from near annual to areas burned only once every few decades (van Wilgen et al. 2003). In 1954, a series of Experimental Burn Plots (EBPs) were established in four regions of KNP as part of a long-term research program—one of the longest-running fire manipulation experiments in Africa—to investigate the effects of fire frequency and season on the park's flora and fauna (Biggs et al. 2003).

Our study was conducted during the wet seasons (November–March) of 2005–2006, 2006–2007, and 2007–2008. We focused our research on the annual and triennial late-winter (August) burn, and unburned control treatments found at each of three EBP blocks (referred to as the Marheya, N'wanetsi, and Satara blocks) located near the Satara rest camp in the central region of KNP (24°23'52" S, 31°46'40" E). Thus, we had a total of nine experimental plots (3 blocks of 3 treatment plots; Appendix: Fig. A1). Each plot is rectangular and averages 9.7 ha in area (range 6.4–16.1 ha). The annually burned plots were burned every year of the study (but failed to burn in 2007–2008 due to low fuel loads), and the triennially burned plots were burned prior to the 2006–2007 growing season but not in 2005–2006 or 2007–2008.

The average annual rainfall in the Satara region is ~550 mm, with the majority of the precipitation falling during the wet season (September–March). Vegetation in the region is comprised of a mixture of C₄ grasses (e.g., *Bothriochloa radicans*, *Digitaria eriantha*, *Panicum maximum*, and *Urochloa mosambicensis*) and woody plants (e.g., *Acacia nigrescens*, *Sclerocarya birrea*, *Dichrostachys cinerea*). The mean fire return interval in this part of KNP is approximately five years, though there is considerable variation across the region (van Wilgen et al. 2000). The central region of KNP supports a diverse assemblage of large mammalian herbivores (Appendix: Table A1) with zebra (*Equus quagga*), wildebeest (*Connochaetes taurinus*), impala (*Aepyceros melampus*), African buffalo (*Syncerus caffer*), giraffe (*Giraffa camelopardalis*), and elephant (*Loxodonta africana*) being some of the most common. The most common large predators in the Satara region of KNP are lions (*Panthera leo*; 12.7 animals/100 km²), hyenas (*Crocuta crocuta*; 13.9 animals/100 km²), leopards (*Panthera pardus*; 3.5

animals/100 km²) and cheetahs (*Acinonyx jubatus*; 2.2 animals/100 km²) (Mills and Funston 2003).

Herbivore surveys

We surveyed the abundance of herbivores on each plot from a vehicle approximately twice weekly throughout the 2005–2006, 2006–2007, and 2007–2008 growing season (November–March), for an average of 27, 37, and 37 surveys per plot each season respectively. Each plot was surveyed from fixed observation points every 60 m (Appendix: Fig. A1) along perimeter fire-breaks. Using binoculars, we scanned for herbivores for 60 seconds at each point and recorded the abundance of each species. Data on gender and age class (adult vs. juvenile) of each individual were also recorded, when possible. The precise location of individuals or each group of herbivores was recorded by noting their compass bearing and distance from the fixed observation point using a laser rangefinder (Bushnell Yardage Pro 500DX). In addition, we recorded the behavior of the herbivores sighted (e.g., foraging, resting, moving, being vigilant), although we did not conduct detailed behavioral observations. When groups of individuals were sighted, we estimated the proportion of each herd performing specific behaviors. Although plot length varied, and hence the number of total observation points, the width of each plot was a constant ~180 m. The constant width of the plots means that the distance from observers on the exterior of the plot to the interior of the plot was always similar (at most 90 m) and that the distance from animals was not confounded across the different burn plots. The timing of surveys was distributed evenly over four three-hour time periods spanning the approximate 12 hours of daylight (6:00–9:00, 9:00–12:00, 12:00–15:00, 15:00–18:00). The density of herbivores per plot was calculated as the total number of herbivores observed per plot divided by the area of the plot in ha.

In 2006–2007 and 2007–2008, we also conducted herbivore abundance surveys at night because many herbivore species have feeding bouts throughout the night (Estes 1991) and because predation risk tends to be higher at night when visibility is lower and predators are more active (Funston et al. 2001). Thus, parsing herbivore distribution by day and night may reveal

important time-dependent differences in habitat use. We sighted herbivores using spotlights by observing the reflected light from their eyes. Because observing this reflection is facilitated by slowly changing angles relative to the herbivore, nocturnal surveys were performed from a vehicle moving at idle speed (~10 km/hour) around the perimeter of the burn plots. When eye reflections were observed, the vehicle was stopped and the herbivores were identified and counted through binoculars and their behavior recorded. The timing of the night surveys was distributed between two time periods spanning roughly 5 hours of darkness in total (21:00–23:30 and 23:30–02:00).

In 2007–2008, we incorporated dung surveys as an additional method to survey relative herbivore use of the different burn plots. Dung surveys are a reliable method to estimate relative use of different areas across a landscape (Barnes 2001). We established 50 m × 4 m transects parallel to the short axis of each EBP block (n = 7 per block). Herbivore dung piles were surveyed and identified to species (Stuart and Stuart 2000) during January, March, and May 2008. Once counted dung was removed from each transect to avoid recounting during subsequent surveys. For dung surveys, we calculated the average number of dung piles per herbivore species per transect for each burn plot averaged across all three survey periods.

Forage quantity, forage quality, and plant community surveys

For each of the burn plots we assessed: (1) herbaceous plant abundance, species richness, and species diversity, (2) aboveground net primary production (ANPP), (3) the abundance of woody vegetation, (4) grass forage quality (crude protein), and (5) soil nutrient concentrations (C, N, P, K, and Na). In October–November 2005, seven octagonal, 7 m diameter herbivore exclosures and adjacent open plots of identical size were established in each burn plot as part of a long-term study to assess the interactive effects of fire frequency and herbivory on herbaceous plant community structure. The exact location of each 7 m diameter exclosure within the fire treatment plots was randomly selected, but constrained to sites dominated by herbaceous vegetation. Each unfenced plot was located

within 10 m of its paired enclosure in a site with similar vegetation.

We surveyed the herbaceous plant community within permanent 4-m² quadrats in each plot at the beginning (December/January) and end (March) of each growing season to capture peak abundance of both early and late-season species. This regime has been used extensively in other studies and has been shown to reliably detect differences in plant community composition among areas differing in fire frequency (Collins and Smith 2006). Each permanent 4-m² quadrat was divided into four 1-m² subplots, and in each subplot, we visually estimated percent aerial cover (to nearest 1%) for each species rooted therein, along with amount of exposed bare ground and plant litter (Collins and Smith 2006). These data were used to calculate the relative percent cover of grasses, forbs, and bare ground, as well as species richness.

We used data on ANPP from clipping three 20 cm × 50 cm quadrats positioned within each enclosure (n = 7) in each growing season from Buis et al. (2009). Because these harvests were from within the enclosures, they represent a standardized estimate of annual plant productivity across all treatments and herbivore densities, rather than the actual resource available to herbivores (McNaughton 1983). Although herbivores can stimulate primary production in some savanna systems (Frank et al. 1998), this mechanism does not appear to function in KNP where ANPP does not differ in enclosures vs. open areas (Knapp et al. 2012). Thus, the primary production from within the herbivore enclosures adequately represents the plant production available to herbivores across the growing season.

To assess woody vegetation abundance, we conducted belt transect surveys during the 2007–2008 growing season. The woody vegetation communities on these burn plots change very slowly and are likely relatively stable given the consistent fire treatments over the past 50+ years of burning (Higgins et al. 2007). Thus, the 2007–2008 transects are likely representative of the woody plant communities in 2005–2006 and 2006–2007. Since the EBP blocks differ in size, one 100 m × 4 m transect was sampled for approximately every 3 ha of plot area, with the number of transects per EBP block varying between three and five. In each transect, all

woody species were identified and their heights measured to the nearest 0.1 m. The total number of individuals either under or over 1.0 m in height on each transect was tabulated, and the mean abundance of each height class per 400 m² was computed for each EBP block. Woody plants were partitioned into these two height classes to parse shorter vegetation, which is unlikely to have an impact on visibility and hence predation risk, from taller vegetation which may be more likely to reduce visibility and influence predation risk for many herbivore species (Riginos and Grace 2008).

To assess forage quality within each burn treatment plot, a sample of green leaf tissue (n = 7 per block) from the representative dominant grasses was taken in mid-March in 2005 and monthly from January–April in 2007 and 2008. These composite grass tissue samples were dried at 60°C for 48 hours and ground in preparation for nutrient content analysis. Total nitrogen was determined via a Carlo-Erba elemental analyzer and multiplied by 6.25 to convert to crude protein. We also analyzed the abundance of important nutrients (C, N, P, Na, and K) in the soils that have been linked to herbivore foraging (e.g., McNaughton 1990) from soil cores taken in areas adjacent to the herbivore enclosures (n = 7) across burn plots in 2005–2006. C and N were analyzed with a Thermo EA1112 C/N analyzer. P was analyzed using the Mehlich-3 phosphorus protocol. Na and K were analyzed using atomic absorption spectrometry.

Lion kills, vegetation characteristics, and predation risk

Between April 2005 and May 2007, five female lions from four prides and two male lions belonging to resident coalitions in the Satara region of KNP were fitted with GPS/GSM collars (African Wildlife Tracking) programmed to record a fix hourly during the night and at four-hour intervals during the day. We identified clusters of GPS fixes (i.e., where lions were relatively stationary) as possible kill sites (Tambling et al. 2010). Suspected kill sites were investigated on foot and the remains of prey species identified, if present. We assumed lion resting status from GPS clusters longer than one hour with no associated kill (Tambling et al. 2010). We assessed the vegetation (tree density

and grass height) surrounding kill sites (May 2005–April 2007) and compared that to vegetation surrounding sites where no remains were found (March 2006–May 2007). We used a five-point scale to assess average grass height at either kill or non-kill sites: (1) ~10 cm tall, (2) ~30 cm tall, (3) ~50 cm tall, (4) ~70 cm tall and (5) >~1 m tall. Likewise, we estimated tree density on a five-point scale as: (1) no trees, (2) low tree density (stems >10 m apart), (3) moderate tree density (stems 5–10 m apart), (4) high tree density (stems 2–5 m apart), and (5) impenetrable tree cover (stems \leq 2 m apart). While these estimates are not as quantitative as the calculated tree densities of the EBPs, the sampling time required made belt transects at the 1340 kill and non-kill sites prohibitive.

Statistical analysis

We used single factor ANOVA's, followed by Tukey's tests for multiple comparisons when appropriate, to test for differences in herbivore density and vegetation characteristics across the different burn treatments. Habitat selection among the three burn treatments was calculated using Ivlev's index (Ivlev 1961), calculated using the equation $E_i = (r_i - n_i)/(r_i + n_i)$ where r_i is the proportion of all individuals of a given herbivore species that were found on the i th type of burn plot and n_i is the proportion of the i th type of burn plot available to herbivores out of the total area represented by all the burn types (i.e., proportion of the total burn plot area made up of the i th type of burn plot; for example annual burns represented 31.5% of the total burn plot area in the study). Confidence intervals (95%) for Ivlev's index were calculated following Strauss (1979). Selection either for or against a burn type was considered significant when the 95% confidence intervals were either above or below zero, respectively.

Follows of lion GPS clusters revealed carcasses of buffalo ($n = 37$), giraffe ($n = 16$), impala ($n = 21$), kudu ($n = 14$), wildebeest ($n = 45$), and zebra ($n = 58$) where tree density and grass height were estimated. Further, we estimated tree density and grass height at 1149 GPS clusters that were categorized as non-kill sites. It is unlikely that tree density would change meaningfully over the time that we investigated GPS clusters so we included data from all sites in comparisons of

tree density between kill vs. non-kill sites. However, due to the temporal variability in the timing of cluster investigation and the ground-truthing of clusters, only those clusters checked within 28 days of occurrence were included in the analysis of grass height. Longer periods between cluster occurrence and examination investigation could have resulted in significant changes to the herbaceous vegetation characteristics. This restriction lowered our replication for sites with grass estimates to buffalo ($n = 28$), giraffe ($n = 11$), impala ($n = 10$), kudu ($n = 9$), wildebeest ($n = 32$), zebra ($n = 41$), and non-kill sites ($n = 556$). We tested for differences in grass height and tree density between lion kill and non-kill sites for each common herbivore species using two-sample t-tests. From within the vegetation data sets for non-kill sites, we randomly chose 30 data points from each of the grass height and tree density estimations to compare with the number of kill sites for each herbivore species. We corrected for multiple tests comparing kill sites to the single set of non-kill site data points using the false discovery rate correction (Verhoeven et al. 2005).

RESULTS

Across all three years of the study, we sighted a total of 4,187 individuals representing twelve different species of mammalian herbivore (Appendix: Table A1). Impala, zebra, and wildebeest were the most abundant herbivores comprising 37%, 28%, and 18% of all herbivores observed, respectively. There were differences in overall herbivore density across burn treatments in 2005–2006 with the highest densities occurring on annual burns (Fig. 1). There were no significant differences in herbivore densities in either 2006–2007 or 2007–2008, but the overall pattern in abundance was similar to that of 2005–2006 with the most herbivores visiting the annually burned and fewer herbivores on the triennially burned and unburned plots. Across years, ~50–60% of the animals observed were actively foraging. Approximately 10% of animals were clearly not foraging and were lying down, standing in shade, or obviously transiting through the plots. The majority of the remaining individuals were likely foraging but were observed when they were being vigilant or pro-

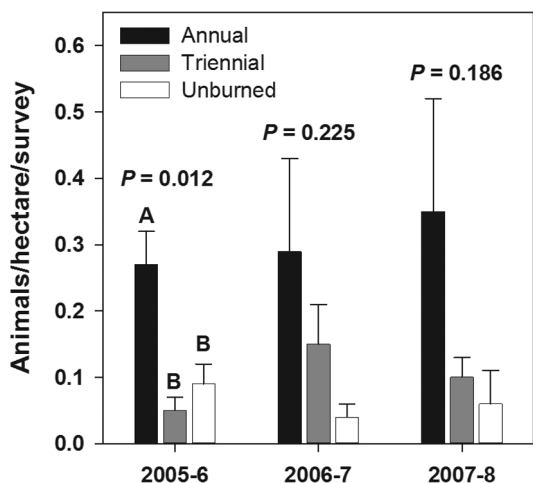


Fig. 1. Mean densities of all herbivores observed on the different fire treatments at Kruger National Park, South Africa, during the three-year study period. Data are means with standard errors. Statistics are from one-factor ANOVA testing for differences among treatments within each year. Letters above bars designate differences as tested for by Tukey's HSD.

cessing food, etc. Thus, foraging appears to be one of the main reasons herbivores selected different habitats although other factors such as social interactions, shade, visibility, and areas for resting also likely influenced habitat selection.

Patterns of selectivity for the different burn treatments appeared dynamic for several herbivores species (Fig. 2). For example, zebra selected for annual burns and against triennial burns and unburned plots in both 2005–2006 and 2007–2008 (Fig. 2D, F, respectively). But, in 2006–2007 zebra showed no preference for either annual or triennial burns while avoiding unburned areas (Fig. 2E). Likewise, impala show complicated selectivity patterns. While consistently preferring triennial burns, impala showed no preference for annual burns in 2005–2006 but selected against these areas in 2006–2007 and 2007–2008 (Fig. 2M–O). Impala also selected against unburned areas in 2005–2006 but used them in proportion to their abundance in 2006–2007 and 2007–2008. In contrast, wildebeest consistently selected for annually burned plots and against triennial burns and unburned areas in every year of the study. Elephant and buffalo were observed but not frequently enough to calculate meaningful selectivity statistics.

On nocturnal herbivore surveys, zebra, wildebeest, and impala represented over 95% of animals identified. As with the diurnal surveys, nocturnal patterns in burn selectivity differed across herbivore species (Fig. 3). In both 2006–2007 and 2007–2008, zebra and wildebeest both strongly selected for annual burns while selecting against triennial burns and unburned plots. In 2006–2007 impala selected for annual burns and against unburned areas while using triennial burns in proportion to their availability (Fig. 3C). In 2007–2008, impala selected for both annual and triennial burns and against unburned areas (Fig. 3F).

Overall, dung surveys of herbivore abundance in 2007–2008 showed relatively similar patterns to driving abundance surveys. For instance, wildebeest selected for annual burns and against triennial and unburned plots according to both dung and driving surveys (Fig. 4E). Yet, for some species such as impala, dung surveys showed contrasting patterns to driving surveys. Dung surveys showed impala not selecting for either annual or triennial burns while avoiding unburned plots (Fig. 4G). Yet, driving surveys in 2007–2008 showed impala either selecting against (diurnal surveys; Fig. 2O) or selecting for (nocturnal surveys; Fig. 3F) annual burns. Dung surveys allowed us to capture distribution information for species that were rarely observed on driving surveys. For example, elephant selected against triennial burns while visiting annual burns and unburned areas in proportion to their abundance (Fig. 4A). Buffalo selected for triennial burns while avoiding annual and unburned plots (Fig. 4C).

There were significant differences in vegetation characteristics across the different burn plots. Grass cover tended to be highest in unburned plots although this pattern was not always significant (Fig. 5A–C). Cover of forbs only differed in 2007–2008 when cover was highest in annual burns, intermediate in triennial burns, and lowest in unburned areas (Fig. 5D–F). Patterns in bare ground cover depended strongly on fire regime and time since burn with annual burns typically having the highest bare ground but with triennial burns having high bare ground when they were burned in 2006–2007 (Fig. 5G–I). Plant litter showed opposite patterns to that of bare ground having highest cover in unburned

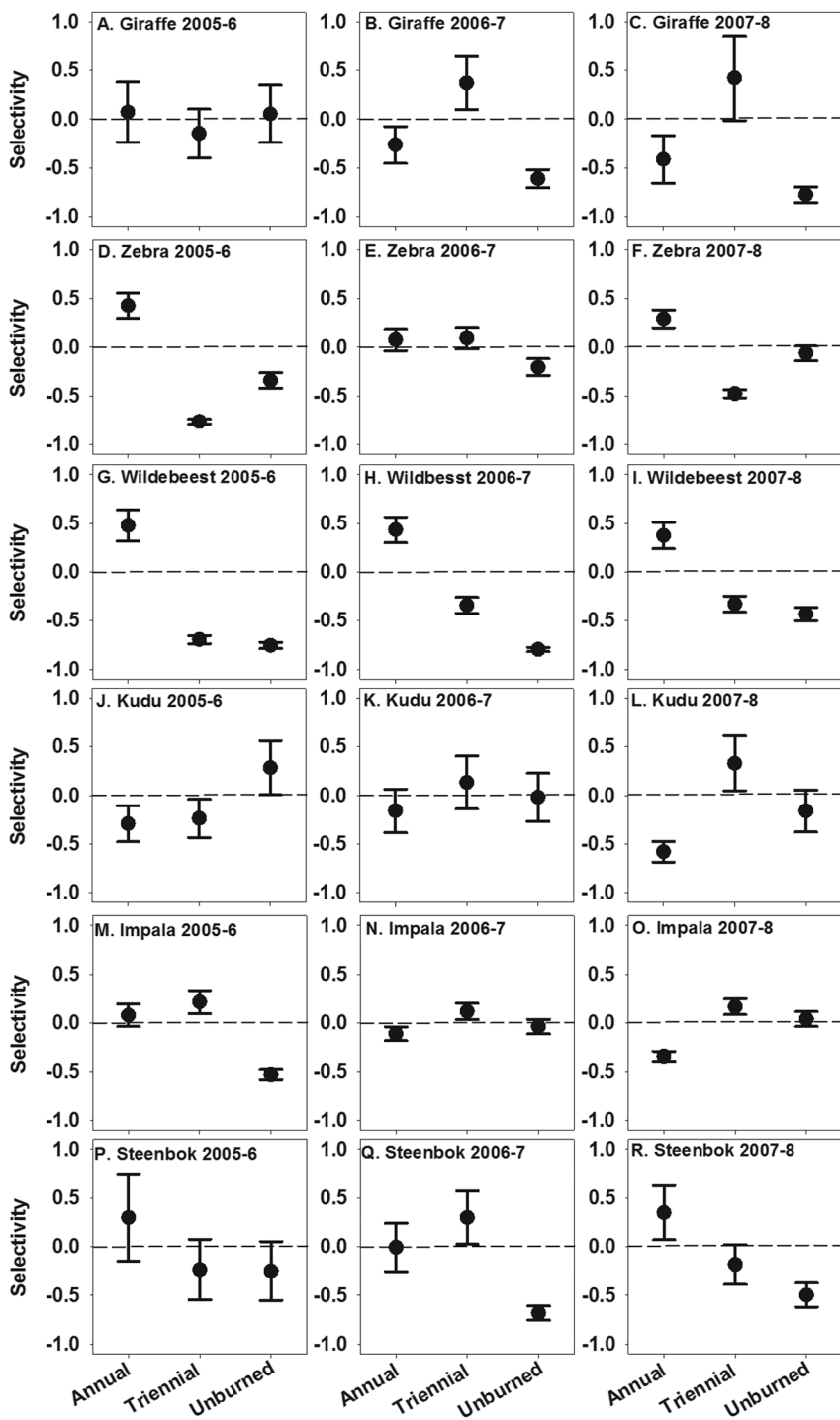


Fig. 2. Ivlev's electivity calculations (see text for details) of different herbivore species for the burn treatments across sampling years for daytime surveys. Data are means and 95% confidence intervals. Positive numbers denote selection for a burn treatment while negative numbers denote selection against burn treatment. Selectivity 95% confidence intervals that cross the zero line were not considered significant. Herbivore species are presented in decreasing order of body size from the top (giraffe) of the figure to the bottom (steenbok).

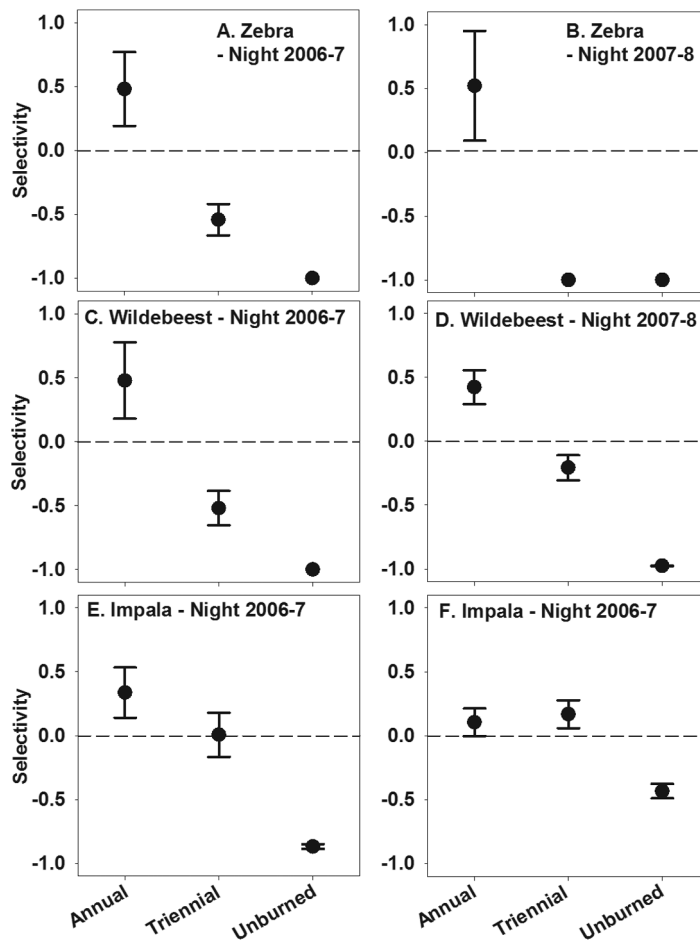


Fig. 3. Ivlev's electivity calculations (see text for details) of different herbivore species for the burn treatments across sampling years for nighttime surveys. Data are means and 95% confidence intervals. Positive numbers denote selection for plots while negative numbers denote selection against plots. Selectivity 95% confidence intervals that cross the zero line were not considered significant. Herbivore species are presented in decreasing order of body size from the top (zebra) of the figure to the bottom (impala).

areas in the triennial burns in 2005–2006 prior to burning in 2006–2007 (Fig. 5J–L). Patterns in plant species richness were variable with 2005–2006 showing the only significant differences with the unburned areas trending towards higher species richness (Fig. 6A–C). There were no differences in ANPP (Fig. 6D–F), crude protein (Fig. 6G–I), or soil nutrients (Appendix: Tables A2 and A3) across burn types. However, there was a trend for grasses in annual burns to have higher crude protein than the other treatments. The density of woody vegetation was highest in unburned areas, intermediate in triennial burns, and lowest in annual burns with

unburned areas having 7 times more and triennial burns 5 times more woody vegetation than annual burns (Fig. 7).

Vegetation surrounding lion kills showed that there were differences in patterns of kills across herbivore species with respect to both grass height and tree density (Fig. 8). Lion kills of buffalo, kudu, and zebra were in areas of taller grass and denser tree cover as compared to sites where kills were not found. Kills of giraffe were found in areas with denser tree cover as compared to areas without kills but showed no difference in grass height with non-kill sites. Sites of impala and wildebeest kills showed no

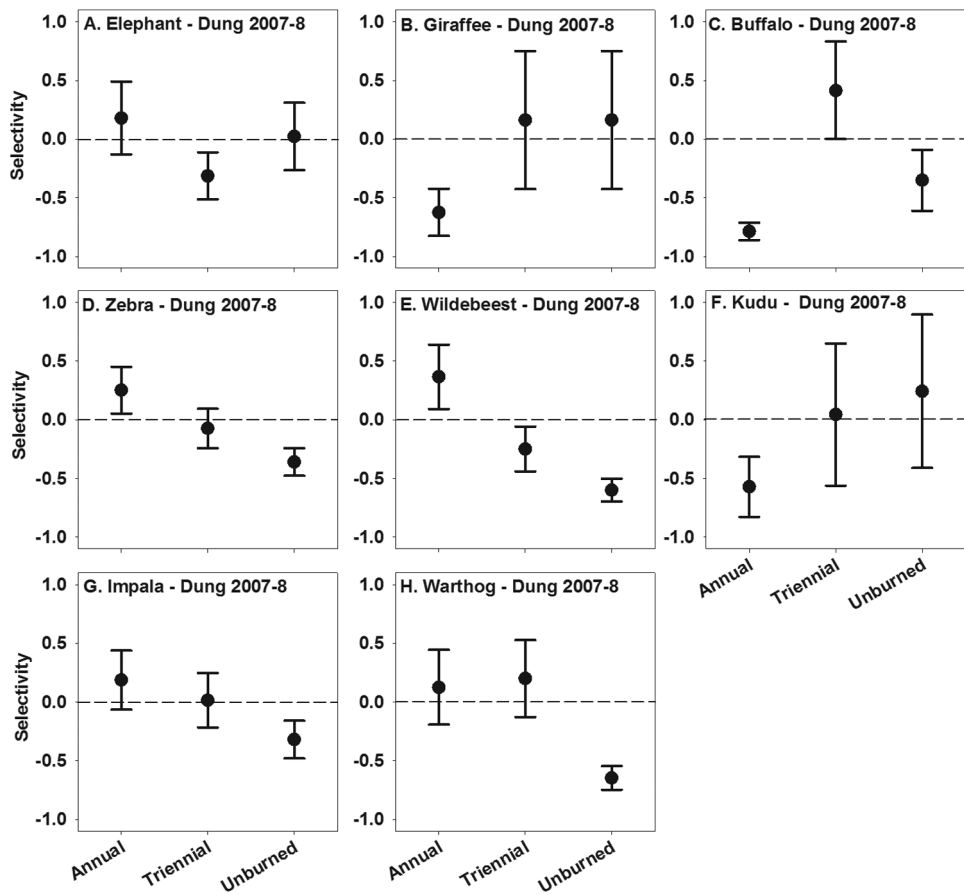


Fig. 4. Ivlev's electivity calculations (see text for details) of different herbivore species for the burn treatments across sampling years for dung surveys in 2007–2008. Data are means and 95% confidence intervals. Positive numbers denote selection for plots while negative numbers denote selection against plots. Selectivity 95% confidence intervals that cross the zero line were not considered significant. Herbivore species are presented in decreasing order of mass from the left to right within a row and top to bottom within a column.

differences in either grass height or tree density as compared to non-kill sites.

DISCUSSION

In this three-year study, we found that large herbivore species differed in their selection of savanna habitats burned at different frequencies, with many of the grazer species selecting for recently burned areas and browsers selecting for infrequently burned areas (Table 1). For example, wildebeest and zebra often selected for annual burns although zebra switched to using triennial burns in the year they were burned (Fig. 2). In contrast to grazers, browsers such as kudu and giraffe and the mixed-feeding impala often

selected for triennial or unburned areas (Figs. 2 and 4), which had significantly more woody vegetation (Fig. 8), though often not more forb cover (Fig. 5), than annual burns. Similar patterns in selection among grazers and browsers have been observed in other studies (Archibald and Bond 2004, Archibald et al. 2005, Sensenig et al. 2010). However, the impact that different top-down and bottom-up processes influenced habitat selection appeared to differ significantly across species.

Many aspects of forage quality (e.g., crude protein, soil nutrients) and quantity (e.g., grass cover or primary production) did not appear important for explaining herbivore distribution, at least for grazers. There were no significant

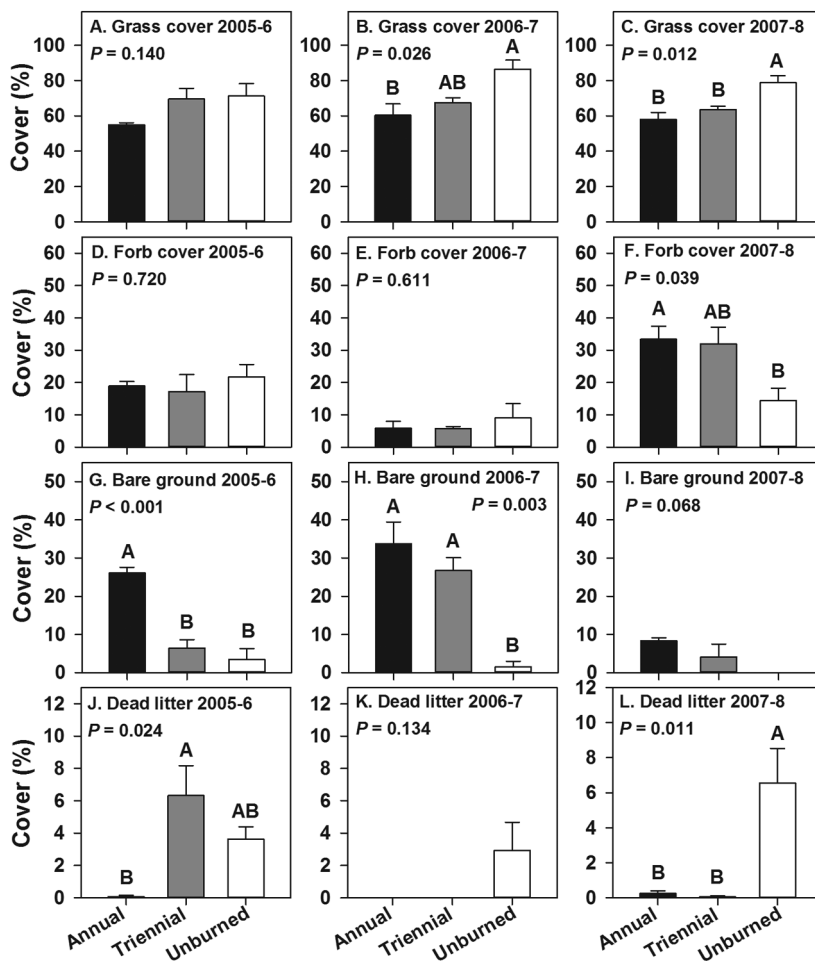


Fig. 5. Percent cover of grass (A–C), forbs (D–F), bare ground (G–I), and dead plant litter (J–L) across burn treatments for each year of the study. Data are means with standard errors. Statistics are from one-factor ANOVA testing for differences among treatments within each year. Letters above bars designate differences as tested for by Tukey's HSD.

differences in grass crude protein (Fig. 6) or measured soil nutrients (Appendix: Table A3) across treatments and grass cover tended to be highest in areas that most herbivores avoided (i.e., unburned areas, Fig. 5). These data are in contrast to other work that suggests that recent burns significantly increase forage quality, specifically crude protein (Sensenig et al. 2010). The 50+ year burning regime in KNP may have limited the potential increase in forage quality as compared to areas that are subject to less frequent burning or a shorter history of burning (Blair 1997). Further, *Bothriochloa radicans*, noted for its poor forage quality (Perrin and Brereton-Stiles 1999), dominated the annual burns (~70%

of grass cover across years), yet many grazers (e.g., wildebeest, zebra, warthog) selected for these plots (Figs. 2, 3, and 4 and Appendix: Fig. A2). It is also important to consider that we may not have adequately captured all of the metrics of forage quality as we did not measure acid detergent fiber or energy content of forage, which may influence habitat selection in ungulates (Fryxell 1991, Fryxell et al. 2004, Sensenig et al. 2010). However, previous years' dead forage, which reduces access to or palatability of current year's green forage (Heitkonig and Owen-Smith 1998), may have been one aspect of fire-driven forage quality that influenced herbivore distribution. Dead plant litter was more abundant on

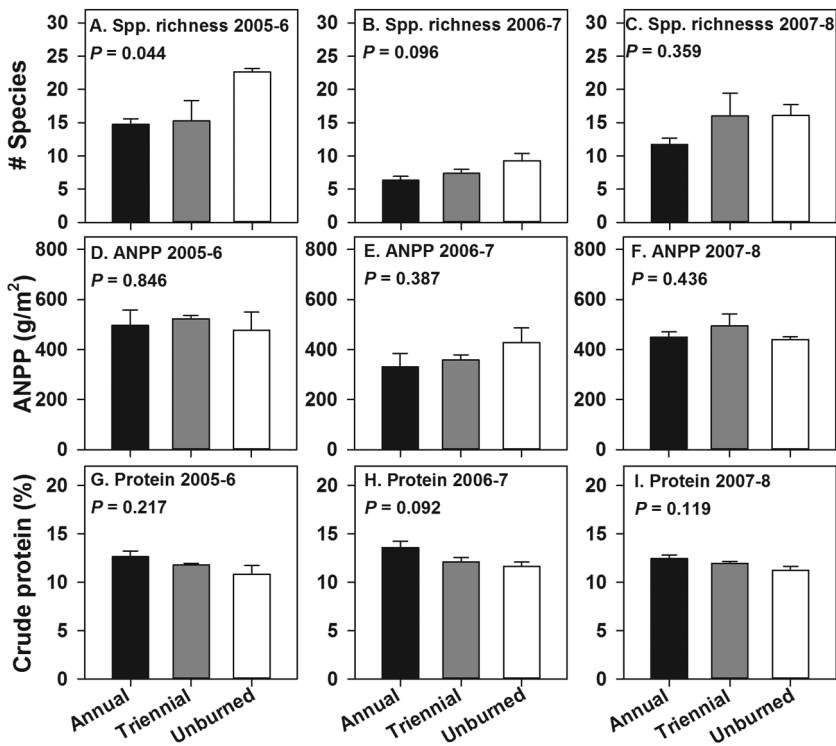


Fig. 6. Plant species richness (A–C), aboveground net primary production (ANPP) (D–F), and crude protein (G–I) across burn treatments for each year of the study. Data are means with standard errors. Statistics are from one-factor ANOVA testing for differences among treatments within each year. Letters above bars designate differences as tested for by Tukey's HSD.

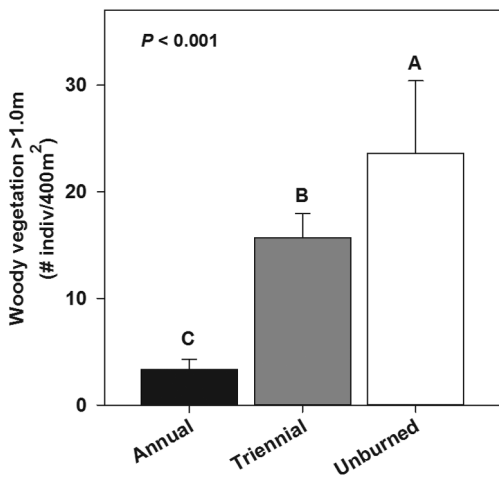


Fig. 7. Density of woody vegetation >1.0 m in height across the different burn treatments in the 2007–2008 season. Data are means with standard errors. Statistics are from one-factor ANOVA testing for differences among treatments within each year. Letters above bars designate differences as tested for by Tukey's HSD.

plots that were selected against by most grazers (e.g., unburned plots and triennial plots except for 2006–2007 when they were burned) and rare on plots selected for (e.g., annual burns and triennial in 2006–2007).

Top-down forces such as predation risk could be an important determinant of herbivore habitat selection particularly if risk of predation varies among habitats with different levels of complexity. As we predicted, lions appeared to have more success in killing several different herbivore species in habitats with complex vegetation (Fig. 8), as others have shown (Funston et al. 2001, Loarie et al. 2013). As a consequence, predation risk appears to force herbivores to trade-off food acquisition for reduced risk of predation. For example, buffalo, which often select habitats with higher forage quantity (Winnie et al. 2008), avoided annual burns with the lowest grass cover and selected for triennial burns (Fig. 4C). However, they selected against

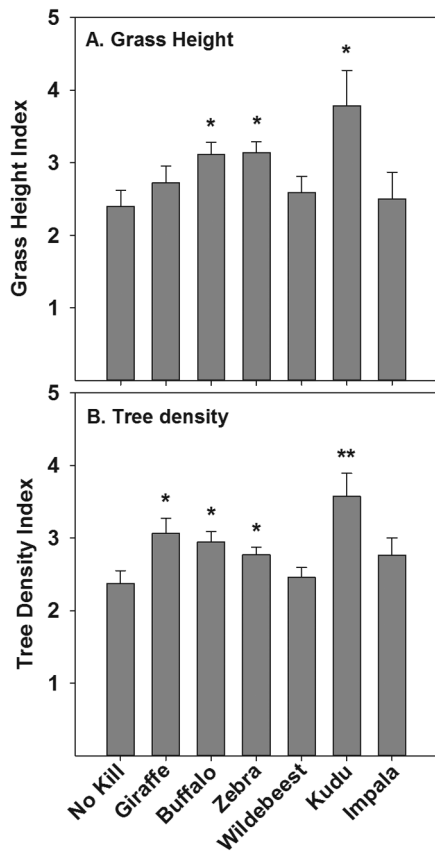


Fig. 8. Comparisons of grass height (A) and tree density (B) indices at sites of lion kills of different herbivore species with sites where no kill was found. A grass height index of 0 = no grass to an index of 5 = grass >1 m in height. A tree density index of 0 = no trees to an index of 5 = tree stems <2 m apart. Data are means with standard errors. Asterisks denote significant differences of the herbivore kills from the ‘No Kill’ sites as determined by two-sample t-test; * $P < 0.05$, ** $P < 0.01$. P -values were corrected for multiple comparisons using the false-discovery rate correction.

unburned areas that had the highest abundance of grasses (Fig. 5) likely because the higher density of woody vegetation (Fig. 7) made them more vulnerable to predation by lions (Valeix et al. 2009, Tambling et al. 2012; Fig. 8).

Similarly, wildebeest consistently preferred annual burns with lower grass abundance as they often prefer shorter, nutritious grasses (Bell 1971, Wilmshurst et al. 1999). Yet in 2006–2007, wildebeest avoided the short, nutritious post-fire grasses on the triennial burns, potentially to limit

their predation risk from foraging in areas with dense woody vegetation. Wildebeest rarely venture into areas with dense woody vegetation (Thaker et al. 2010), potentially to limit predation risk, but our data did not show that wildebeest carcasses were more likely to be found in areas with taller grass or denser woody vegetation (Fig. 8). These data do not necessarily mean that areas with tall grasses and dense woody vegetation are not dangerous to wildebeest as they may avoid these areas in order to maximize their preferred forage and minimizing their risk of encounter with predators. Browsers such as giraffe also showed similar trade-offs as they chose triennial burns over unburned areas (Fig. 2B, C) even though unburned areas have a higher density of preferred forage (i.e., *Acacia* spp. trees). However, these same trees also likely increase potential predation risk from lions (Thaker et al. 2011; Fig. 8) suggesting a strong trade-off between food and predation risk.

Trade-offs between foraging and predation also likely drove the strong diurnal vs. nocturnal dynamic in habitat selection exhibited by several herbivores. During the day, zebra appeared most strongly influenced by forage characteristics as they frequently used annual burns and used recently burned triennial plots in proportion to their abundance in 2006–2007, despite the more complex vegetation (Fig. 7) that makes them more vulnerable to predators (Fig. 8). However, at night, when lions are most active and make the most successful kill attempts (Funston et al. 2001), zebra appear less willing to make riskier choices and strongly selected against the more heavily vegetated triennial burns and for the safer annual burns.

Differences in escape tactics may translate into differences in the perceived and actual risk of predation for herbivores (Lima 1992, Wirsing et al. 2010), with agile species being more willing to risk foraging in areas with thicker woody vegetation where they can outmaneuver potential predators. In our study, the mixed-feeding impala frequently used both the triennial burns and unburned areas, which gave them a greater flexibility in diet choice given the diversity of herbaceous and woody vegetation that exists on these plots. However, impala kills were not associated with taller grasses or denser woody vegetation (Fig. 8). Thus, the nimble impala

Table 1. Overall trends in habitat preferences, preferred habitat traits, and potential trade-offs in avoiding predation risk for common herbivores during diurnal and nocturnal observations and dung counts. N/A = insufficient sample size for meaningful evaluation.

Common name	Mass (kg)	Guild	Diurnal selection	Nocturnal selection	Dung selection	Preferred habitat traits	Predation risk trade-off
Steenbok	10	Browser	Annual, Triennial (when burned)	N/A	N/A	Low to intermediate woody plant density	Avoids densest woody browse in unburned
Impala	50	Mixed feeder	Triennial, Unburned	Annual, Triennial	Annual, Triennial	Significant variation depending on context	Shifts away from dense vegetation in unburned at night
Warthog	80	Grazer	Annual, Triennial (when burned)	N/A	Annual, Triennial	Low woody plant density, much bare ground	No obvious trade-off
Blue wildebeest	250	Grazer	Annual	Annual	Annual	Low woody plant density, much bare ground	Avoids nutritious forage in triennial post burn
Kudu	250	Browser	Triennial, Unburned	N/A	Triennial, Unburned	Intermediate to high woody plant density	No obvious trade-off
Plains zebra	300	Grazer	Annual, Triennial (when burned)	Annual	Annual, Triennial	Low woody plant density, much bare ground	Shifts away from intermediate woody plant density at night
African buffalo	700	Grazer	N/A	N/A	Triennial	Intermediate woody plant density, high grass biomass	Avoids highest grass biomass on unburned
Giraffe	1200	Browser	Triennial	N/A	Triennial, Unburned	Intermediate woody plant density	Avoids densest woody browse on unburned
African elephant	5700	Mixed feeder	N/A	N/A	Annual, Unburned	Low or high woody plant density	Not at risk of predation

seems to be at less risk of predation by lion in habitats with denser woody vegetation relative to larger herbivore species. Even so, at night, impala switch to preferring annual burns and consistently avoiding unburned areas (Fig. 3E, F). Although our relatively coarse-scale analysis of vegetation at impala kill sites revealed no apparent predation advantage for lions in dense vegetation, a recent assessment of kill sites in KNP using high resolution LIDAR (light detecting and ranging) measurements shows that male lions are more successful at killing impala in dense vegetation (Loarie et al. 2013). These data support our assessment that unburned areas are indeed risky for impala at night. Thus, impala appear to be trading food for safety by avoiding the riskiest habitats with the highest woody vegetation cover at night when predators are most active and detection of predators is likely most difficult. Differences in trade-offs between food and safety between day and night may be a

common theme across herbivore species; however the natural history of the different species (e.g., diet, body size, escape tactics) likely shape the specific nature of these trade-offs.

Studies often use either dung surveys or diurnal observations of herbivores to document patterns of habitat selection. (e.g., Riginos and Grace 2008, Valeix et al. 2009, Sensenig et al. 2010). However, our use of both diurnal and nocturnal surveys suggests that using only daytime observations or dung surveys may miss important patterns in habitat selection. For example, diurnal surveys alone underestimated use of annual burns by both impala and zebra, which utilize them primarily at night. Further, dung surveys in 2007–2008 showed that impala used annual and triennial burns in proportion to their abundance, but avoided unburned areas. Yet visual surveys showed that impala selected against annual burns and used unburned areas in proportion to their abundance during the day,

but selected for annual burns and against unburned areas at night when predators were most active. Thus, using direct observations of herbivores during both day and night gives a more complete and nuanced view of habitat selection that cannot be inferred from dung counts alone. We encourage more studies to incorporate nocturnal surveys of herbivore distribution as limiting observations to daylight hours may miss the strongest signal of predation risk on habitat selection.

Habitat selection is often a hierarchical choice with different processes operating at different scales from the landscape down to local levels (Senft et al. 1987), and the scale of our study may have influenced which processes most shaped habitat selection. For example, herbivores track forage quality across 10s or 100s of kilometers (McNaughton 1990). Further, herbivores often appear to select areas of the landscape at the km² scale based on available forage or forage quality or greenness (Bhola et al. 2012). Thus, the fact that we did not see a strong and consistent impact of forage quantity or quality on habitat selection may be because of our local rather than landscape scale focus. Consequently, we may have detected a strong impact of predation risk because we worked at the local scale where a choice between high vs. low risk habitats must strongly minimize encounter rates with predators and maximize the ability to escape predators once an encounter happens.

Although herbivores can choose to forage in less risky habitat to reduce exposure to predators, as we show here, increasing vigilance, or apprehensive foraging, is another way that herbivores can minimize risk while still exploiting potentially risky habitats (Smith and Cain 2009, Pays et al. 2012). Had we conducted detailed behavioral studies, we may have shown that herbivores may increase their vigilance at the expense of foraging time in order to exploit potentially riskier habitats. For example, impala using the densely-vegetated unburned areas may have taken fewer bites per unit time as compared to feeding rates in more open habitats in order to spend more time scanning for predators in the riskier habitat. Thus, we may have underestimated the trade-off between foraging and predation avoidance as we did not conduct detailed behavioral observations of herbivores. Including

studies of vigilance and foraging would have given us a more complete picture of how herbivores deal with gathering food versus avoiding predation.

In summary, trade-offs between lowering predation risk and acquiring quality forage are common across ecosystems and a unifying concept for predator-prey interactions (Brown and Kotler 2004). In African savannas, there are often interspecific differences in how top-down (predation risk) or bottom-up (forage quality/quantity) forces impact population regulation and habitat selection of herbivores (Hopcraft et al. 2010, Thaker et al. 2011). In our three-year study, we show that for herbivores in Kruger National Park, South Africa both predation risk and access to appropriate forage are important drivers of habitat selection and that fire frequency can mediate these forces. These trade-offs differed among species depend on herbivore body size, escape tactics, preferred diet, and time of day. Our work adds to a growing body of literature across disparate ecosystems suggesting that herbivores often choose to limit predation risk even if it often means utilizing areas with lower quality foraging habitat (e.g., Creel et al. 2005, Wirsing et al. 2007, Riginos and Grace 2008, Hebblewhite and Merrill 2009).

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SUPPLEMENTAL MATERIAL

APPENDIX

Table A1. Mammalian herbivores (>5 kg) observed on the Experimental Burn Plots in the central region of Kruger National Park. The number of individuals of each species reported is based on the total observations for all study plots combined. Average number of surveys per plot per year were $n = 27$ in 2005–2006 and $n = 37$ in both 2006–2007 and 2007–2008.

Herbivore species	Scientific name	Biomass (kg)†	Feeding guild	Common predators‡	No. individuals		
					2005–2006	2006–2007	2007–2008
Steenbok	<i>Raphicerus campestris</i>	10	Browser	Cheetah, hyena	24	61	43
Grey duiker	<i>Sylvicapra grimmia</i>	15	Browser	Cheetah, leopard	2	0	0
Impala	<i>Aepyceros melampus</i>	50	Mixed feeder	Lion, hyena, cheetah, leopard	305	604	648
Warthog	<i>Phacochoerus aethiopicus</i>	80	Grazer	Lion, leopard	35	97	105
Blue wildebeest	<i>Connochaetes taurinus</i>	250	Grazer	Lion	165	254	335
Kudu	<i>Tragelaphus strepsiceros</i>	250	Browser	Lion	58	57	24
Waterbuck	<i>Kobus ellipsiprymnus</i>	260	Grazer	Lion	1	0	1
Burchell's zebra	<i>Equus quagga</i>	300	Grazer	Lion	265	328	579
African buffalo	<i>Syncerus caffer</i>	700	Grazer	Lion	3	31	12
Giraffe	<i>Giraffa camelopardalis</i>	1200	Browser	Lion	44	60	23
White rhinoceros	<i>Ceratotherium simum</i>	2200	Grazer	N/A	1	3	0
African elephant	<i>Loxodonta africana</i>	5700	Mixed feeder	N/A	5	8	6

†Biomass estimated for the average individual from each species from Estes (1991).

‡Common predators from Mills and Funston (2003).

Table A2. Soil nutrient characteristics of experimental burn plots. Data are means with standard errors in brackets. Soils were sampled in 2005–2006 season.

Burn	Soil N	Soil C	Soil P	Soil K	Soil Na
Annual	0.14 (0.01)	2.29 (0.13)	80.58 (12.06)	588.14 (39.99)	41.14 (6.24)
Triennial	0.15 (0.02)	2.39 (0.38)	62.69 (7.01)	589.57 (50.98)	44.62 (5.00)
Unburned	0.17 (0.02)	2.48 (0.34)	67.28 (8.40)	584.90 (62.68)	44.52 (5.69)

Table A3. Results of one-factor ANOVA testing for differences among burn treatments in concentration of different soil nutrients.

Nutrient	df	F	P
Carbon	2	0.098	0.908
Nitrogen	2	0.983	0.445
Phosphorus	2	0.977	0.429
Sodium	2	0.002	0.998
Potassium	2	0.122	0.887

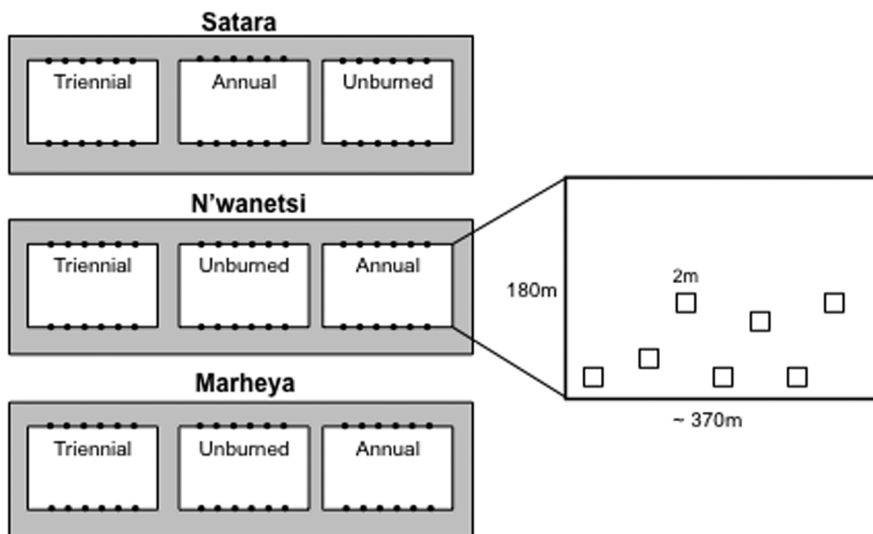


Fig. A1. Layout of experimental burn plots (EBPs) and herbivore and vegetation surveys at the three study blocks (Satara, N'wanetsi, Marheya) in the Kruger National Park. Black dots represent fixed herbivore survey points, and small boxes the vegetation sampling quadrats (boxes are not to scale). The landscape surrounding each block was burned approximately every five years, and the fire-breaks (shown in gray) between each burn treatment plot were burned annually and graded to ensure vehicle accessibility. For simplicity, our focal treatment plots are shown here adjacent to one another, however, in many cases there were additional burn treatment plots (such as those with 6-yr or 2-yr burn frequencies) positioned between our focal plots.

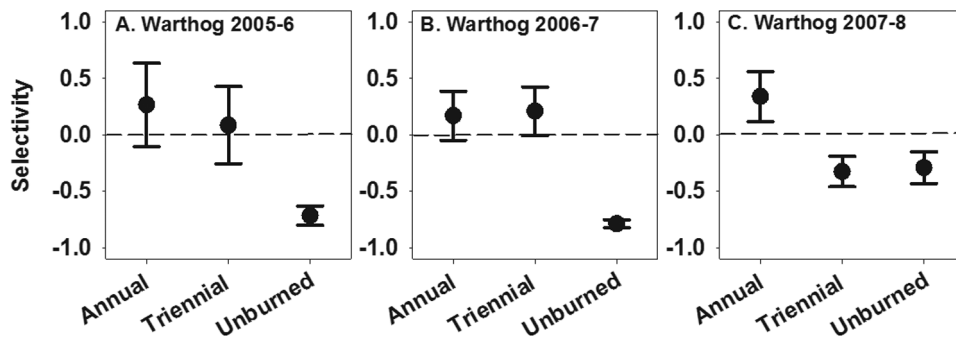


Fig. A2. Ivlev's electivity calculations (see main text for details) of warthog for the burn treatments across sampling years for daytime surveys. Data are means and 95% confidence intervals. Positive numbers denote selection for a burn treatment while negative numbers denote selection against burn treatment. Selectivity 95% confidence intervals that cross the zero line were not considered significant.