

The landscape-scale drivers of herbivore assemblage distribution on the central basalt plains of Kruger National Park

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Abstract

The distribution and abundance of herbivores in African savannas are constrained by interactions between abiotic and biotic factors. At the species-level, herbivores face trade-offs among foraging requirements, vegetation structure, and the availability of surface water that change over spatial and temporal scales. Characterising herbivore requirements is necessary to the management of the environment in which they occur, as conservation management interventions such as fencing and artificial water provision consequently have effects on how herbivores address these trade-offs. We tested the effects of environmental attributes on the probability of presence of herbivore functional types at different distances to water in the Satara section of Kruger National Park over the period of a year. Hypotheses about species' relative distribution and abundance were developed through a literature review of forage and water availability constraints on feeding preference and body size of herbivore biomass. We expected strong seasonal relationships between vegetation biomass and quality, and biomass of water-dependent herbivores with increasing distance to water. Our analyses of herbivore distribution across the region confirmed broad-scale descriptions of interactions between forage requirements and water availability across a set of species which differ in functional traits.

Introduction

Large mammalian herbivores form an essential component of the natural environment in which they occur due to the impact that they have on the structure and functioning of ecosystems (Hempson *et al.* 2015). Their preference for certain habitat types is determined by complex interactions between external factors including forage availability and quality, water availability, soil type, topography, season and predation risk (Bailey *et al.* 1996, O'Kane & Macdonald, 2018). Furthermore, intrinsic factors such as feeding type and morphology interact with resource competition, habitat requirements and facilitation, affecting species-richness and the structure of herbivore assemblages (Cromsigt *et al.* 2009, Gordon & Illius, 1996).

Herbivores select the habitat in which they feed over several temporal and spatial scales. At broader spatial extents, dispersal or migration may be necessary due to constraints of water availability, forage abundance, competition and thermoregulation, whereas at smaller extents these constraints include topography, distance from water, forage quality and quantity, and predation (Bailey *et al.* 1996). Along the body size spectrum, the quality of forage becomes less important than quantity of forage due to the digestive constraints of smaller herbivores (Demment & Soest, 1985). As a result, smaller herbivores exert larger search efforts compared to larger herbivores to find higher quality forage (Bailey *et al.* 1996). Forage quality is affected by soil nutrient content (Holland & Detling, 1990), season and regrowth as a response to herbivory and/or fire (Wilsey, 1996). Finally, the feeding type of herbivores is also closely related to their water dependency, with grazers and mixed feeders experiencing higher levels of water dependency than browsers (Hempson *et al.* 2015).

The constraints under which herbivores select habitat interact with predator avoidance. In areas of diverse herbivore and predator body sizes, smaller herbivores are exposed to a greater risk of predation than larger herbivores, as both small and large predators can consume small-bodied prey (Hopcraft *et al.* 2010). Gregariousness of the species and body size affects predator-avoidance strategies, and herbivores may select more open or dense habitats dependent on the anti-predator strategies they employ (Creel *et al.* 2005, Riginos & Grace, 2008). Herbivores are therefore regulated by top-down (predation) or bottom-up (forage quality and availability) processes (Hopcraft *et al.* 2010). These processes however may not be mutually exclusive. The underlying environmental gradients at the larger scale - soil, climate, water availability and their subsequent effect on forage quality and quantity- is therefore the primary constraint on herbivore distribution across the landscape (Bailey *et al.* 1996, Hopcraft *et al.* 2010).

The complexity of interactions between these processes underpins the importance of understanding savanna ecology to management. Substantial contributions to this understanding have been made by the rich history of monitoring and research which has emerged over the last century from Kruger National Park (hereafter KNP) (Biggs, 2003). KNP has a vastly heterogeneous landscape with diverse herbivore assemblages, facilitating the study of trade-offs herbivores face across multiple spatial and temporal scales. However, one of the primary environmental gradients which determines herbivore distribution, water availability, has been contentious in the context of KNP due to extensive water provision policies (Pienaar, 1997, Smit *et al.* 2007). In 2003, KNP had less than 8% surface area further than 5 kilometres (km) from water (Gaylard *et al.* 2003). This resulted in an observable decrease in grasses and woody cover closer to artificial water points, the decline of rare

herbivores due to an increase in predators, and fluctuations in common herbivore population numbers (Brits *et al.* 2002, Gaylard *et al.* 2003, Harrington *et al.* 1999). Due to these effects, KNP management revised their water provision policy and began to close waterholes across the landscape (Pienaar, 1997).

Considering the increasing decline in global herbivore populations (Ripple, Newsome *et al.* 2015, Vie, Hilton-Taylor *et al.* 2009), it is critical that a comprehensive understanding of the drivers of herbivore distribution across landscapes be developed. The study aims to test whether herbivores follow previously described trends across the Satara landscape, and to test effective means of measuring the determinants of herbivore biomass within certain habitats across a set of species which differ in functional traits. Herbivore studies typically classify species into groups of similar traits (Hempson *et al.* 2015, Shipley, 1999), and this provides a baseline against which to evaluate broad-level trends across different feeding types and body sizes of herbivores. Using these trends, we tested the effect of habitat attributes on eleven herbivore species at the Satara section of KNP. Herbivore studies typically look at aspects of the effects of environmental attributes on herbivores, whereas our study aims to test a combination of aspects across scales and seasons on an herbivore assemblage which differs in functional traits. We have thus tested a number of hypotheses related to the body size and feeding type of these herbivores against habitat attributes: (1) we expected risk of predation to be a stronger predictor of space use by small-bodied herbivores than larger herbivores; (2) we expected feeding type to be a strong predictor of increased daily herbivore presence in relation to distance from water because grazers tend to be more water-dependent; (3) we expected the daily presence of medium-bodied grazers and small mixed-feeders to increase at higher quality forage, and large grazers increasing at

higher quantity forage; and (4) we expected a strong effect of season on the biomass of grazing and mixed-feeder herbivore distribution across the landscape, with biomass and distribution decreasing further from water in the dry season and the reverse for the wet season.

Methods

Study area

This study was conducted in the Satara section (central basalt plains) of KNP, which is situated at the north-eastern corner of South Africa (24.01°S, 31.49°E). Satara receives a mean annual rainfall of 547 mm (February *et al.* 2013). The region experiences mean minimum temperatures of 10°C and 20°C and mean maximum temperatures of 26.3°C and 32.6°C in July and December respectively (Parr, 2008). The vegetation is characterised by *Senegalia nigrescens/Sclerocarya birrea* tree savanna (Gertenbach, 1983). Habitats of this area are attractive to herbivores as two ephemeral rivers, the N'wanetsi and Sweni rivers, typically flow once or twice in the wet season and have a number of pools which may persist in the dry season. Furthermore, surface water may take longer to evaporate on the clayey basaltic soils of the region, resulting in water being more locally available across the landscape in the wet season in the form of pans (Gaylard *et al.* 2003). The Letaba basalt soil type contributes to study area suitability, as it has higher calcium carbonate (CaCO₃) concentrations, which gives rise to extensive grassy plains (Venter, 1986) that are dominated by highly palatable grass species such as *Urochloa mosambicensis* and *Digitaria eriantha* (O'Connor & Pickett, 1992). The area is also exposed to occasional wild-fires and prescribed burns (Van Wilgen *et al.* 2004).

Site design

Suitable sites were identified by mapping distance to water, soil type and vegetation type as buffers of 0.5 km, 2.5 km and 5 km from all surface water (rivers and artificial waterholes), overlaid across the soil and habitat type layers using ArcGIS v10.5. Site suitability was characterised by relative distance to water, soil type, habitat type, accessibility and the absence of previous experimental manipulation. Six sites were placed at three different distances to water, sites 0.5 km from water were situated north of the N'wanetsi river and 2.5 km and 5 km from water south of the N'wanetsi river (Figure 1). Five of the six sites fell within the Satara land type in KNP, dominated by *Senegalia nigrescens*/*Sclerocarya birrea* tree savanna, but due to constraints of site suitability one of the six sites fell within the Mavumbye habitat type, a similar land type characterised as *Senegalia nigrescens* bush savanna (Gertenbach, 1983). Sites were sampled in June 2017, October 2017, February 2018 and June 2018, resulting in three sets of data from the late dry, early wet and late wet seasons. Wildfires occurred throughout the sampling period, resulting in one site at 2.5 km burning patchily in June 2017, and both 5 km sites burning completely in November 2017.

Each site comprised of six 20x20 m plots, 100 m apart, each fitted with a Cuddeback Attack Interchangeable Flash (Blue Series, Model 1255) camera trap. Plots were set up as part of a study on patch scale selection by herbivores. Camera trap data was thus the combined trapping effort of six cameras per site, each totalling an approximate area of 3.12 ha. We are confident that the plot treatments have not affected our evaluation of these landscape scale patterns, as the scale at which this paper is focused is inherently inclusive of patch scale selection in some species (Cromsigt & Olff, 2006, Pretorius, 2009). Camera trapping is an effective, non-intrusive and replicable means of surveying mammals over a wide range of

environmental and temporal scales (Carbone *et al.* 2001), allowing a novel means to overcome observational error of dung counts or animal observation counts.

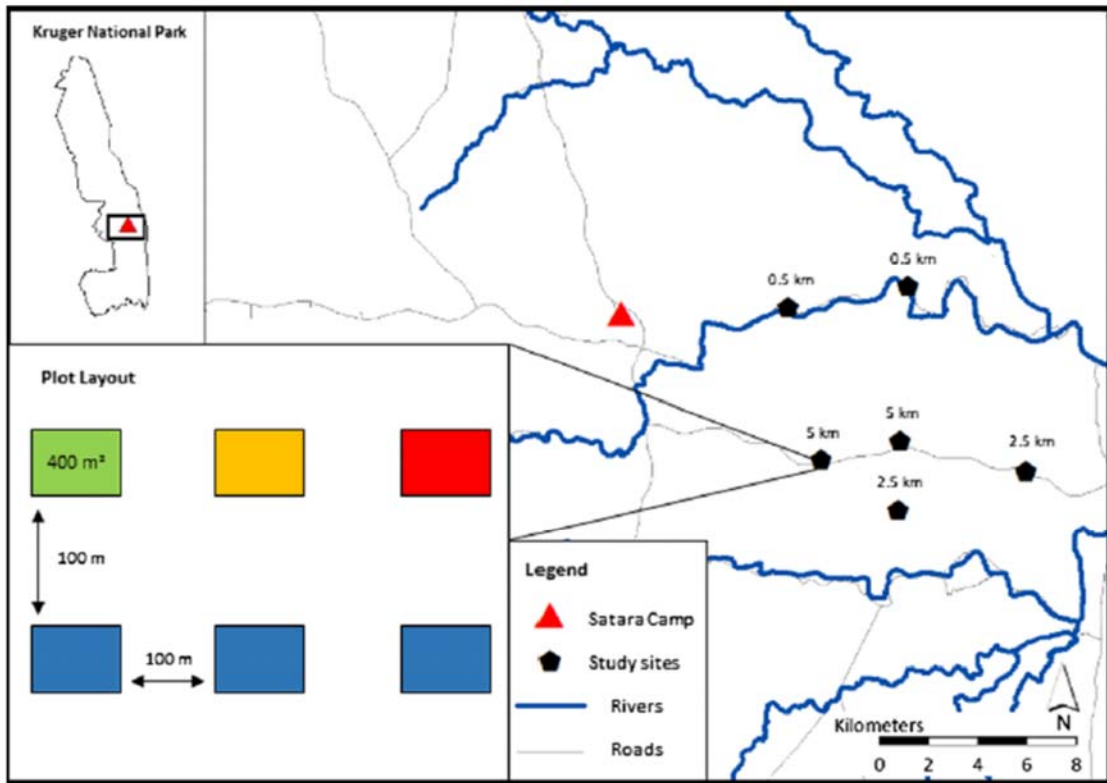


Figure 1: Map of the Satara section where the study was conducted, relative to the Satara Rest Camp. The site layout reads as follows: green plot= mown; yellow= mown and fertilised; red=fertilised only; blue=control. Plots were placed approximately 100 m apart and were 400 m² in size.

Camera traps were fitted to each plot to have the best visual of the 400 m² plot area and were placed between 0.5 m and 1 m from the ground. They were angled away from the sun where possible, and set to a wide view angle, Fresnel cover lowered and at a wide aspect. The camera traps were set to take photographs at 10-minute intervals when activity was sensed. Finally, they were serviced (batteries replaced, and data retrieved) every three months, but batteries lasted on average five weeks, resulting in five weeks of data per season.

Herbivore biomass

The broad spatial and seasonal trends assessed in this study focused on water availability, forage constraints and habitat requirements of the herbivore species which commonly occur in the Satara region of KNP. These herbivore species were selected due to their representation of a suite of feeding preferences and body sizes, and the quantity of data collected by camera traps. The herbivore species were thus: five grazers (blue wildebeest *Connocheates taurinus*, Burchell's zebra *Equus quagga burchelli*, buffalo *Syncerus caffer*, waterbuck *Kobus ellipsiprymnus*, white rhinoceros *Ceratotherium simum*); four browsers (common duiker *Sylvicapra grimmia*, giraffe *Giraffa camelopardalis giraffa*, greater kudu *Tragelaphus strepsiceros*, steenbok *Raphicerus campestris*); and two mixed feeders (elephant *Loxodonta africana* and impala *Aepyceros melampus*). Attributes were assigned to camera trap data as follows: date; species within the photo; number of individuals; time of day; functional characteristics (body size, feeding preference and digestive type), hereafter functional types. Feeding preference followed the three generalist functional classifications of ungulate herbivores: namely grazer, browser and mixed feeder (Gordon *et al.* 1996; McNaughton & Georgiadis, 1986, Owen-Smith & Novellie, 1982). Counts data from captures were converted to the midpoint of the body weight range per species as described by Clauss *et al.* (2003). As biomass values for size classes small and large were low due to low detection by camera traps, these size classes were merged with small-medium and medium-large respectively. Biomass duplications for species which remained at the site for the period of more than one hour were removed from data prior to analysis.

Environmental covariates

Distance to water was the primary determinant of site placement as it typically dictates herbivore movement (Gaylard *et al.* 2003) and seasonal population fluctuations of herbivore

species in savanna systems. The distance from the N'wanetsi and Sweni rivers, and the associated waterholes of the area, were used to determine suitable sites of the three distances from water. Predation was measured through camera trap data, allowing covariates of predator species, incidences of multiple predators and days since predator presence to be measured. Lion photo captures were also recorded as an individual variable due to the strong influence they have on foraging and vigilance behaviour of a range of herbivore body sizes (Périquet *et al.* 2012, Valeix *et al.* 2009). Camera trap data was also used to determine grass height (using a marked pole in front of each camera), and plot burn data (burnt/unburnt and days since fire).

The average distance to the nearest visual obstruction was measured as a proxy for landscape of fear, given that distance to the nearest obstruction changes risk of ambush by a predator and anti-predator strategies employed by herbivore species. This value was the mean of measurements to the nearest obstruction (trees or shrubs) on each plot, using a range finder at a height of 1.5 m every 15°, totalling 24 measurements (Riginos, 2015). The inverse of these measures was used to determine the distance between trees.

The following environmental variables were taken on each plot at each data collection period to measure forage quantity and quality: grass biomass using a disc pasture meter (Trollope & Potgieter, 1986), for which the measurement value was used as a representation for biomass; grass quality using the Walker eight-point scale (Walker, 1976); and grass species were identified and a percentage cover within the plot estimated using Braun-Blanquet measure (Westhoff & Van Der Maarel, 1978). The percentage of vigorous grass cover was determined using the mean of 'vigorous' values measured with the Walker eight-point scale (Walker, 1976), and used as a proxy for foliar protein using the assumption that

low biomass, green grass had a higher protein content (Arsenault & Owen-Smith, 2008). Percentage available browse was assigned using height classes and tree counts (Riginos, 2015). The coefficient of variation (CV) for grass biomass values was used as a measure of biomass heterogeneity, and the CV of distance to the nearest obstruction as landscape heterogeneity.

Data analysis

Camera trap data in our study had a high proportion of zeros, even when aggregated into night and day periods. We thus decided to first work on a presence/absence data to determine which environmental variables have the strongest effect on the species composition of the herbivore community. We estimated the probability of presence of a given species or functional group, using generalised linear model for binomial data. We then investigated the drivers of biomass structure of the community by testing the variables associated with the relative biomass of the various functional groups, using presence data. We used a generalised linear model to analyse the determinants of daily observed biomass values per species and functional group biomass values for species with sufficient occurrence data for models to produce robust results. Biomass data were log-transformed to reduce large variance generated through high heterogeneity in body size, allowing data to conform to parametric analyses. All analyses were performed using R packages v3.4.1.

The dredge function in package MuMIn (Bartoń, 2014) was applied to the most complex models for both binomial and biomass data to generate subsets of the fixed effects of the global model. Models with AICc values which differed by < 2 were then averaged using the model.avg function (Appendix A, Appendix B). Some variables retained in the average model

gave estimates that had very large standard errors including 0; they were subsequently removed to simplify the final model.

Predation data was insufficient to determine an effect of predation on daily biomass. Data was initially split according to five time periods; namely pre-sunrise (00h00 to 05h59), morning (06h00 to 09h59), midday (10h00 to 13h59), afternoon (14h00 to 17h59) and night (18h00 to 23h59). In the process of determining whether predator incidence was sufficient to have an effect on herbivore presence and biomass for 24 hours thereafter (Valeix *et al.* 2009), presence/absence and biomass values for night and day were created by merging the relevant time of day classes together. There was no significant effect of predator occurrence on any of the functional types, and we thus do not present analysis with predator incidence in the result section, but we will briefly comment on this observation in the discussion.

Results

Probability of occurrence

Feeding types

Binomial data models overall produced results (Table 1, Appendix C) which followed expected trends from literature. Probability of grazer presence decreased with increasing distance from water, with the effect increasing in the dry season (Fig. 2a). For grazers, distance additionally interacted with grass biomass, and grazer probability of presence increased with higher grass biomass further from water (Fig. 2a). We expected an increased biomass of grazers on burned sites than unburned sites, however burn effects were not selected within the 'dredge' process and thus did not have an effect on the overall grazer functional type.

Table 1: A summary of the expected outcomes and results produced by GLMs for binomial data for each functional type, indicating the probability of presence by a functional type at certain habitat attributes. Species traits and expectations were based off the following literature: Gagnon *et al.* 2000, Clauss *et al.* 2003, Arsenault *et al.* 2008, Hempson, Archibald *et al.* 2015.

Functional Type	Expected outcome	Predictor variable	Result
Grazer	Occur close to water; select for quality forage	Grass biomass	Select for quality close to water; select for quantity further from water. Preference for burned areas
Mixed Feeder	Select for browse in dry season and grass in wet season	Grass biomass	Low presence further from water and in increased grass height
Browser	Occur further from water; select dense habitat	CV distance to nearest obstruction	As expected
Small-Medium herbivore	Occur closer to water; select forage for quality	Grass height	Occur at higher grass height and further from water
Medium herbivore	Occur closer to water; select forage for quality	CV distance to nearest obstruction	As expected
Medium-large herbivore	Occur closer to water; select for quantity	Grass height	Higher probability of presence further from water at increased grass height in dry season; higher probability of presence closer to water at decreased grass height in wet season.
Megaherbivore	Occur closer to water; select for quantity	Grass height	Occur further from water; select for short grass height

For mixed feeders, distance did not have effects on probability of presence unless in interaction with grass biomass, and overall probability of presence was lower at higher grass biomass and at greater distance from water (Fig. 2b).

Browser probability of presence increased with increasing distance from water and this effect remained consistent across seasons (Fig. 2c, Fig 6d). Across all distances from water, probability of browser presence was lower on burnt sites (Fig. 2c). Overall, probability of browser presence was lower in the late wet season when compared with late dry and early wet seasons (Fig. 2c, Fig. 2d).

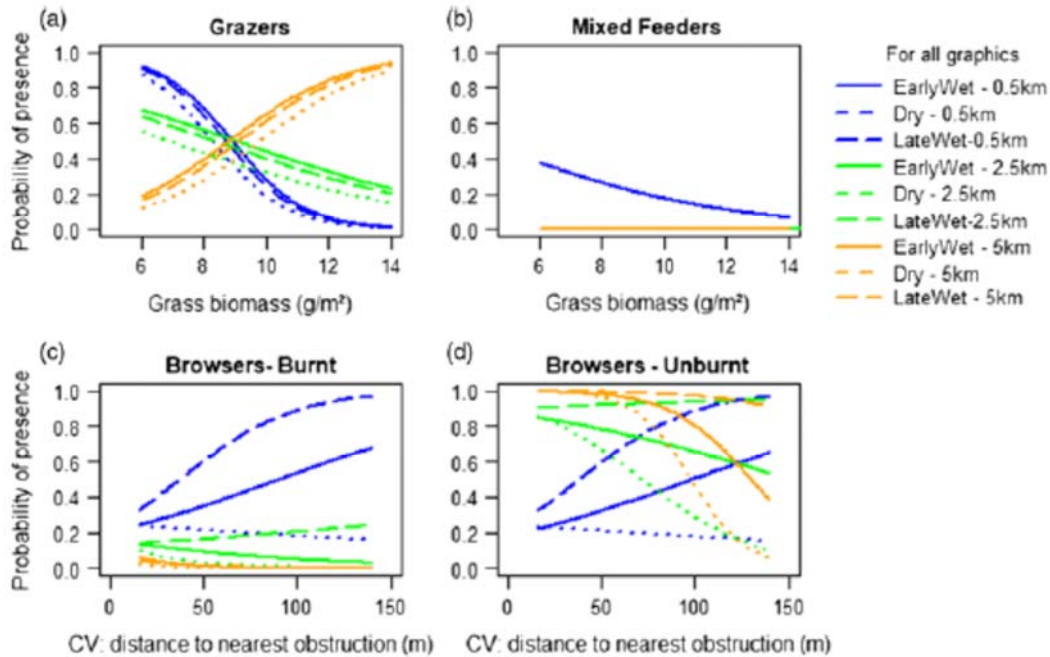


Figure 2: Model simulation over the relevant gradients for the results of each feeding type's estimated coefficients in the Generalised Linear Model (Appendix A – Binomial values; feeding types). Values represented indicate the probability of occurrence by each feeding type predicted by the relevant environmental variables. For mixed feeders, season was not a valid descriptor of biomass; thus, values were lumped to only have three curves representing distance from water. Blue curves represent 0.5 km from water; green represents 2.5 km from water and orange represents 5 km from water.

Body size

For all body sizes, except medium-large herbivores, probability of presence was lower with increasing distance from water (Fig. 3, Fig. 4). For small-medium herbivores, probability of presence increased at higher grass heights (Fig. 3a).

Medium herbivore probability of presence decreased with increasing CV (distance to nearest visual obstruction), i.e. landscape heterogeneity (Fig. 3c, Fig. 3d). Additionally, CV and distance from water interacted, with medium herbivore probability of presence increasing at

higher CV further from water. Probability of medium herbivore presence was higher on burned than unburned sites, decreasing with distance from water (Fig. 3c).

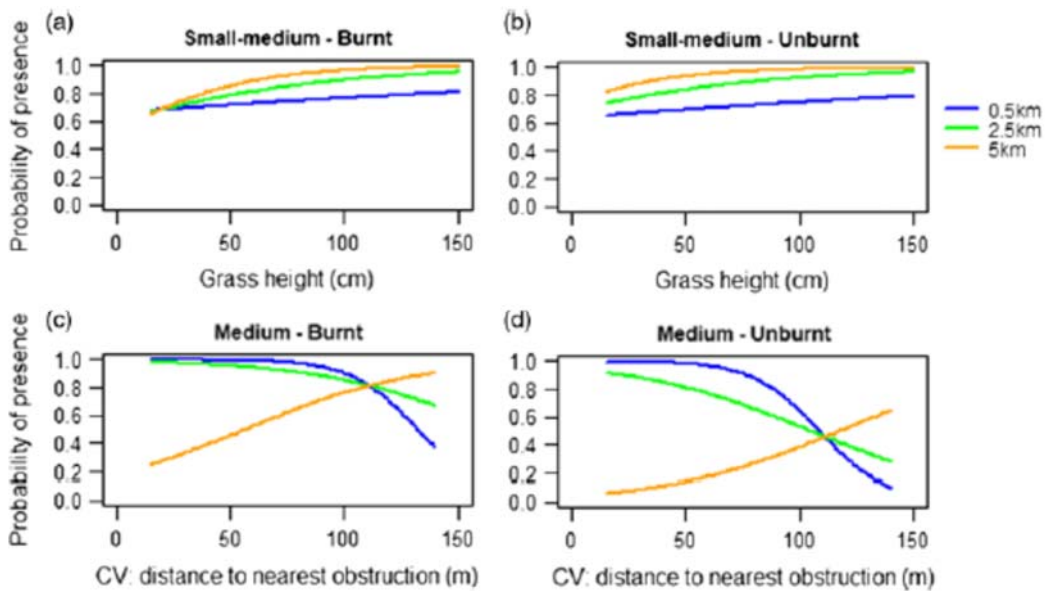


Figure 3: Model simulation over the relevant gradients for the results of each body size’s estimated coefficients in the Generalised Linear Model (Appendix A – Binomial values; body size classes). Values represented indicate the probability of occurrence by small medium and medium sized herbivores predicted by the relevant environmental variables. Blue curves represent 0.5 km from water; green represents 2.5 km from water and orange represents 5 km from water.

Probability of medium-large herbivore presence was highest on areas of burned, short grass height, particularly in the early wet season (Fig. 4a), decreasing with increased distance from water. The inverse was true for unburned areas, with medium-large herbivore presence being highest further from water (Fig.4b). Probability of presence increased with increasing distance from water in the late-dry and late-wet seasons (Fig. 4a, Fig. 4b).

For megaherbivores, probability of presence was highest further from water and at decreased grass height (Fig. 4c).

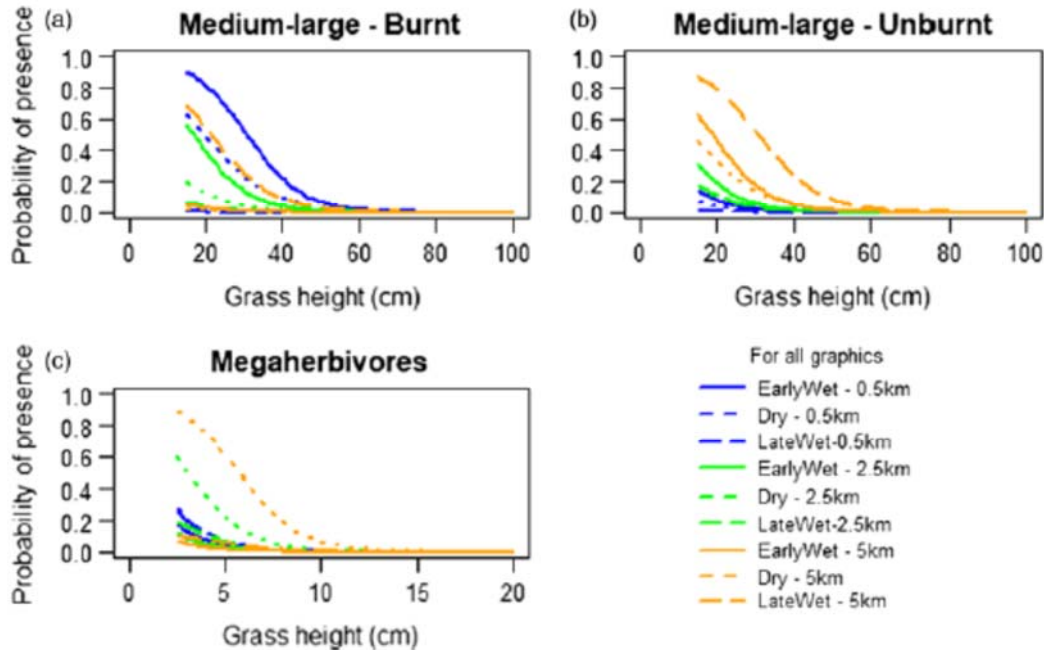


Figure 4: Model simulation over the relevant gradients for the results of each body size's estimated coefficients in the Generalised Linear Model (Appendix A – Binomial values; body size classes). Values represented indicate the probability of occurrence by medium-large sized and megaherbivores predicted by the relevant environmental variables. Blue curves represent 0.5 km from water; green represents 2.5 km from water and orange represents 5 km from water.

Daily biomass results

Feeding types

Daily biomass models revealed that grazer biomass decreased closer to water when grass biomass was lower and increased further from water when grass biomass was higher (Fig. 5a, Appendix D). Mixed feeder biomass was highest at unburnt sites (Fig. 5b). Browser biomass was overall higher further from water and increased with higher CV (distance to the nearest visual obstruction) in the early-wet and late-wet seasons (Fig. 5c, Fig. 5d).

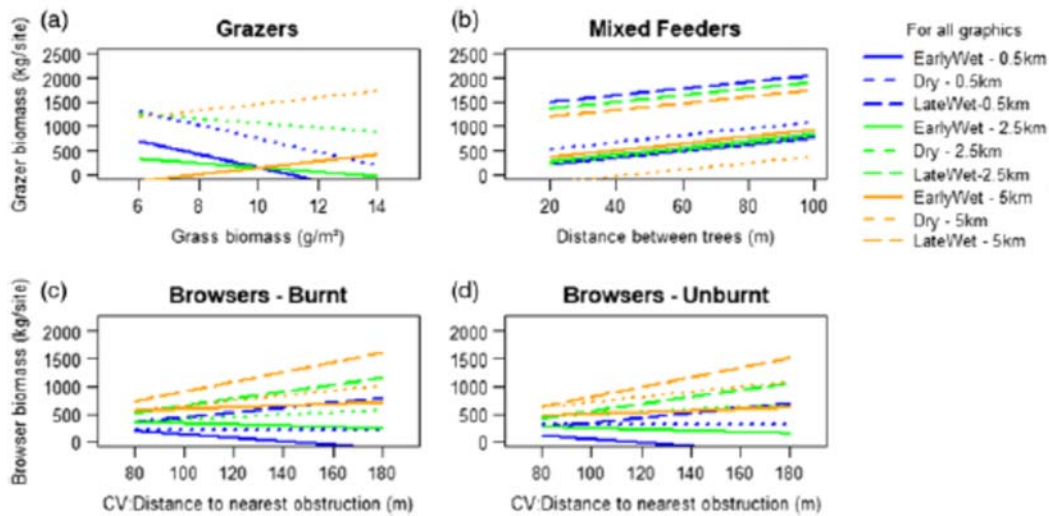


Figure 5: Model simulation over the relevant gradients for the results of each feeding types estimated coefficients in the Generalised Linear Model (Appendix B – Biomass values; feeding types). Values represented indicate the biomass by each feeding type in relation to the functional type’s relevant describing environmental variable. Blue curves represent 0.5 km from water; green represents 2.5 km from water and orange represents 5 km from water.

Body size

Small medium-herbivore biomass was lower in the dry season than early- and late-wet seasons, was highest closer to water and increased with increasing CV (Fig. 6a). Medium herbivore biomass was highest in the early wet season and highest further from water (Fig. 6b). Furthermore, medium herbivore biomass increased with increasing CV at 2.5 km and 5 km from water but remained the same across all CV values at 0.5 km from water (Fig. 6b).

Medium-large herbivore biomass was higher in the early- and late-wet seasons and closer to water on both burned and unburned sites (Fig. 6c, Fig. 6d). Medium-large herbivore biomass decreased with increasing distance between trees at 2.5 km and 5 km from water on both burned and unburned sites, remained consistent at all distances between trees at 0.5 km on burned sites, and decreased again slightly on unburned sites at 0.5 km (Fig. 6c, Fig. 6d).

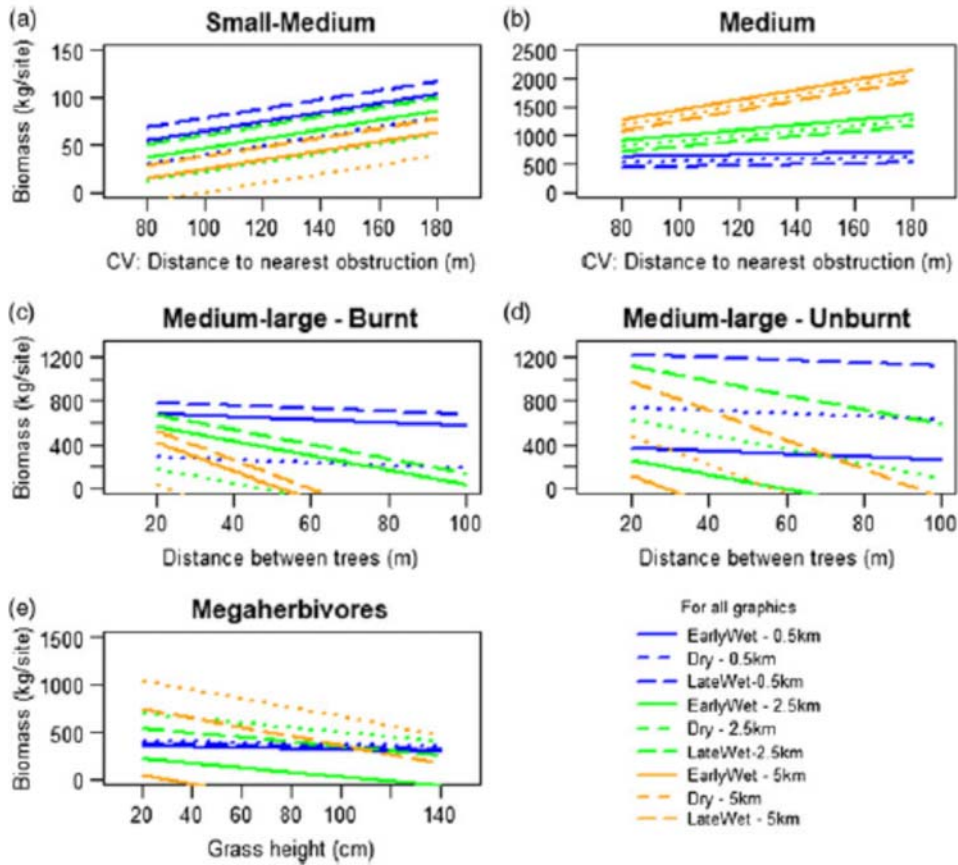


Figure 6: Model simulation over the relevant gradients for the results of each body size's estimated coefficients in the Generalised Linear Model (Appendix B – Biomass values; body size classes). Values represented indicate the biomass by each body size group in relation to the functional type's relevant describing environmental variable. Blue curves represent 0.5 km from water; green represents 2.5 km from water and orange represents 5 km from water.

Megaherbivore biomass was overall higher in the late-wet season than late-dry and early-wet seasons (Fig. 6e).

In terms of assemblage composition, determined by habitat overlap, large changes in abundance and distribution of small mixed feeders and large grazers (Fig. 7) were observed as a result of resource availability.

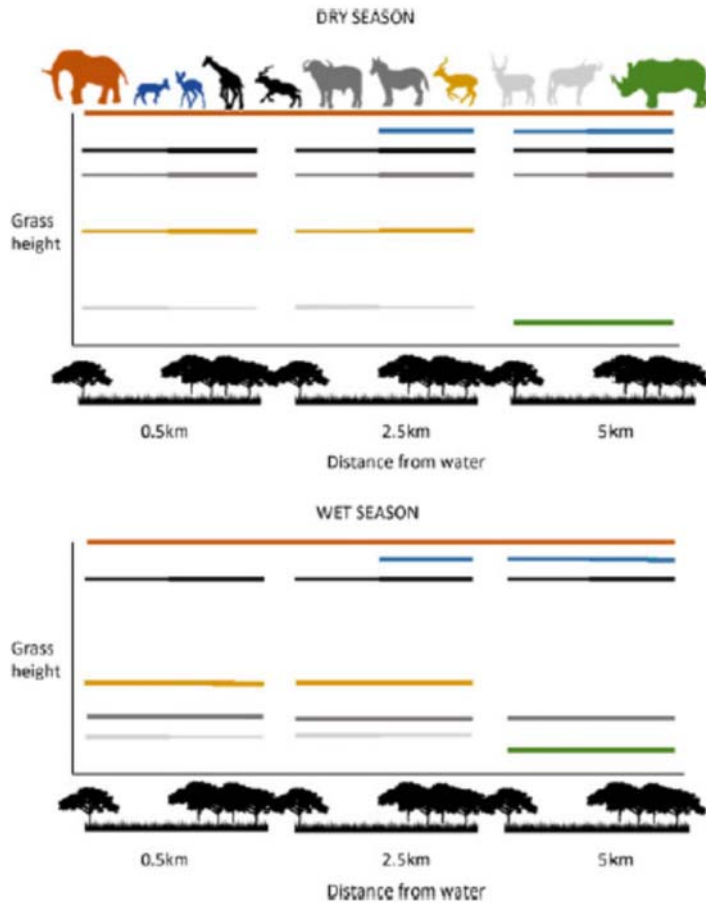


Figure 7: A visual representation of the assemblage composition across the three distances from water for the wet and dry season, and under two types of habitat density. Single trees on the left of each distance represent open habitat and multiple trees on the right represent dense habitat. Thickness of the line represents strength of the probability of presence by the functional types described by species of the same colour. Orange lines = megaherbivore, mixed feeder; Dark blue = large browser; light blue= small browser; black= megagazer; medium grey=large grazer; light grey= small-medium grazer.

Discussion

Grazers

Medium and medium-large grazing herbivores are commonly described as water-dependent, typically being found in the 0.5 km to 2 km zone from water (Gaylard *et al.* 2003). They are comparatively more dependent on surface water than browsing species, as

the moisture content of grass generally falls below 10% in the dry season (Kay, 1997). Although the home range of grazing herbivores is typically closer to water during periods of drought, buffalo, waterbuck and zebra (medium-large body size class) generally occur further than 2.5 km from water (Gaylard *et al.* 2003). Grazing large herbivores alter their distribution to occur further from water to mitigate poor forage conditions (i.e. forage constraints are more important than that of being close to water) (Gaylard *et al.* 2003, Venter *et al.* 2015). Our results show that grazers are attracted to short grass resources closer to water, whereas further from water species are attracted to high grass biomass resources which have not yet been depleted. This indicates that distance from water is a critical determinant of foraging selection patterns by species of different feeding preferences. Additionally, grass growth stage is a critical parameter of preference for a site (Murray & Brown, 1993). Accordingly, grazers will return to sites at previously-grazed areas which are green with palatable regrowth (Archibald, 2008). Our results supported this, with grazer biomass being higher at lower grass biomass at 0.5 km and 2.5 km. Furthermore, grazer biomass was highest at 2.5 km in the early wet season, following the typical magnet effect post-fire regrowth has on the distribution of grazing herbivores (Archibald *et al.* 2005). Forage constraints remained the primary determinant of herbivore biomass across the landscape in the wet season— with clear preference of burnt and shorter grass areas. Finally, distance from water and grass regrowth may be a good reflection of the relationships between grazers and grass biomass, given that body size interacts with whether grazers select forage for quality or quantity, and areas of forage reserve are typically maintained further from water.

Browsers

Our models did not produce conclusive results regarding the relationship between browser biomass and the availability of browse across the landscape, and at a local scale, the relationship between browsing species and the height of browse availability described by Owen-Smith (1985). However, our results supported evidence that browsers are typically less water-dependent and feed > 3 km from water (Gaylard *et al.* 2003). It is worth noting that the browser functional type spanned across three body size classes: namely small (common duiker and steenbok), medium (kudu) and megaherbivore (giraffe), but the effect of distance from water remained consistent with browsers typically occurring further away from water. This may be more true for common duiker, steenbok and kudu, as giraffe typically feed within 0.5 km and 1 km from water (Gaylard *et al.* 2003) despite being a less water-dependent species. These effects however may not be clear in our results due to the confounding nature of the body size classes within this functional type. Browsers occupy habitat further away from water due to higher moisture content of browse compared to grass (Western, 1975). The relationship between browser habitat occupancy and distance to water may also be as a product of the nature of the landscape. Shrub density typically increases with distance from watering points at Satara, with woody vegetation resources having been largely depleted by large herbivores as far as 2.8 km from water (Brits *et al.* 2002). Giraffe and steenbok occupy mixed-habitat, and kudu and common duiker occupy closed habitat for most of the year (Pérez-Barbería *et al.* 2001). However, larger species are able to use a higher diversity of habitat types and are less constrained by dietary tolerance and habitat specificity than smaller species (Du Toit, 2003). Our environmental covariates did not define habitats as closed-, mixed- or open-habitats, however the positive relationship

between browser biomass and the distance to the nearest visual obstruction indicates that browsers we focused on prefer denser areas.

Mixed feeders

Mixed feeders are able to effectively change the utilisation of grazing versus browsing resources across seasons, grazing predominantly in the wet season and browsing in the dry season. In Kruger, mixed feeders are observed to 'switch' from a preference of predominantly graze to browse when the 2-month concurrent mean annual rainfall has dropped below ~30 mm (Du Toit, 2003). Although it is expected that there would be a clear trend between distance to water and mixed feeder biomass, as both species are water-dependent (Redfern, Grant *et al.* 2003), our model results did not show any clear trends, possibly due to high variation across the sample size. This could potentially be because the body size classes in this functional type spanned from small-medium (impala) to megaherbivore (elephant). Impala show preference to feeding within 1-2 km of water (Gaylard *et al.* 2003) with a preference for green grass when rainfall is not limiting (Sinclair & Norton-Griffiths, 1995). Impala will revert to browsing in the dry season when green grass is not available (Du Toit, 2003), as browse maintains a higher protein content for longer into the dry season than grass (McNaughton *et al.* 1986). This was supported by our results in that probability of mixed feeders was higher at shorter grass heights in the wet season when regrowth would be green. This result is likely not representative of elephant biomass, as they experience a weak relationship with forage quality, but a stronger relationship with forage quantity (Redfern *et al.* 2003). Impala will take 2-3 day intervals between drinking although this interval can become twice as frequent in the dry season. Although elephant have shorter drinking intervals (1-2 days in the dry season) than impala, and typically feed in the riparian zone (Gaylard *et al.* 2003), their feeding preference range extends as far as 3 km

from water (Smit *et al.* 2007). Overall biomass trends indicate that there is an increase in mixed feeder biomass in the wet season, likely caused by higher elephant biomass in the region in the late wet season especially when elephants display increased movement across the landscape, as the constraints of forage and water availability are not as severe as in the dry season (De Knecht *et al.* 2011).

Body size classes

Smaller herbivores have higher metabolic constraints than large herbivores due to increased energy demands (McNaughton *et al.* 1986) and their body size furthermore governs the rate and extent of energy which can be extracted from their diet. This is as a result of the retention time of food causing digestion efficiency to be lower in smaller animals than larger animals given the same food source (Demment *et al.* 1985), and thus smaller bodied species must shift to the higher protein diet provided by browse (McNaughton *et al.* 1986). Our results supported evidence that forage is the primary determinant of small-medium herbivore biomass. However, our results also indicated that smaller bodied herbivores prefer areas of increased grass height. This is in contradiction of theory that smaller herbivores, which are more susceptible to predation (Sinclair, Mduma *et al.* 2003), would choose more open habitats to improve predator visibility (Riginos *et al.* 2008). Small herbivores are usually solitary or in pairs (Hempson *et al.* 2015), and are not able to use aggression or speed to prevent predation and thus rely on crypsis in more dense vegetation as an anti-predator strategy (Jarman, 1974). Our models could not test against the effects of predation, and we therefore cannot speculate as to whether risk of predation would be a stronger driver of small herbivore biomass, rather than forage preference. In terms of preference for increased grass height, it is also likely that this pattern is more representative of small bodied browsers (steenbok and common duiker) (Pérez-Barbería *et al.* 2001), rather than

the small-medium bodied impala in the wet season. This pattern will be representative of all three species in the dry season, however impala feeding preference will shift to short, green grass in the wet season as previously discussed.

For medium herbivores, the strongest predictor of biomass at a site was whether it had burnt or not, and also the homogeneity of the landscape. The medium body size class comprises wildebeest and kudu, and thus some results may be confounding. The preference for burnt areas is likely representative of wildebeest biomass, which is well documented throughout the literature (Hassan *et al.* 2007, Shackleton, 1992, Tomor & Owen-Smith, 2002, Wilsey, 1996). In times when burnt regrowth is not available, water availability may be a stronger determinant of wildebeest biomass at a site, as they typically feed in 0.5-1 km zone, despite having longer intervals of 2-3 days between drinking. The burnt areas were at 2.5 km and 5 km from water, indicating that forage quality may be a stronger driver of wildebeest biomass than distance from water. Kudu are water-independent and typically feed > 3 km from water (Gaylard *et al.* 2003), and thus the relationship between decreasing medium herbivore biomass and distance from water is also more likely representative of wildebeest than kudu. Results which are not confounding however, are the relationship between distance to water and coefficient of variation on the distance to the nearest obstruction (Fig. 4). Kudu are likely more representative of the 2.5 km and 5 km trend, occurring at higher biomass in denser areas (which had a higher coefficient of variation), as they are classified as species which prefer closed habitat (Pérez-Barbería *et al.* 2001). The function remains relatively flat for the 0.5 km zone, suggesting that homogeneity of the landscape, both in structure and composition, is not as important a driver of wildebeest biomass as forage quality and water availability.

Our results support findings that preference for burnt areas does not decrease with body size (Klop *et al.* 2007, Tomor *et al.* 2002), contrary to Wilsey (1996). Preference for burnt areas was evident in small-medium, medium and medium-large body size classes. In addition to preference of burnt areas, medium-large herbivores had a clear preference for areas of short grass (Fig. 4). This is especially clear at the burnt 2.5 km zone in the early wet season, when medium-large biomass is at its highest. This further indicates that forage quality and quantity is a stronger driving factor for where medium-large biomass occurs, rather than water availability, as all the three species in this body size class (buffalo, zebra and waterbuck) typically feed in the 0.5 km-2 km zone from water (Gaylard *et al.* 2003). Medium-large herbivore biomass is highest in the late wet season, suggesting that there are population-level movements across the park when water is less easily accessible. This is likely explained by buffalo distribution in the park across seasons, as buffalo typically move further away from water sources in the dry season to meet forage requirements of quantity rather than quality (Redfern *et al.* 2003). This could also explain the relationship between grass height and biomass at the 5 km zone (Fig. 3), although our model for binomial data does not then adequately explain the effects of season, as this trend would only make sense in the dry season. Finally, medium-large herbivores were at higher biomass with decreased distance between trees, where they might have been compelled to feed in areas of higher forage quality (le Roux *et al.* 2018). Forage quality is likely higher because grass layer growth may be facilitated by increased nutrient availability as a result of increased tree density (Ludwig *et al.* 2004).

Results for megaherbivores could not be clearly interpreted as the functional type comprises all three feeding preferences, namely giraffe (browser), white rhinoceros (grazer) and elephant (mixed feeder). Furthermore, elephant and white rhinoceros are classified as

water-dependent species, whilst giraffe are water independent (Gaylard *et al.* 2003, Hempson *et al.* 2015), creating complex interactions with forage requirements and habitat type preference. Our model results indicated that the strongest predictor of megaherbivore biomass was the presence of short grass at 2.5 km and 5 km. This pattern could be explained by forage utilisation by white rhinoceros, as they prefer feeding on short grass areas (McNaughton *et al.* 1986, Pretorius, 2009, Waldram *et al.* 2008). The relationship between grass height and distance from water at 0.5 km indicates that grass height was not a valid predictor of megaherbivore biomass close to water, where giraffe are most likely to feed (Gaylard *et al.* 2003).

Finally, assemblage composition differed across season as a result of altered forage use by the small-mixed feeder and large grazer functional types. In the wet season when resource quality is improved and water is more uniformly distributed across the landscape (Gaylard *et al.* 2003), the abundance of grazers and mixed feeders increases. Furthermore, the change in resource quality causes small mixed feeders and large grazers to alter their resource use from browse and tall grass swards respectively, to short grass swards which contain less fiber and increased crude protein (Arsenault & Owen-Smith, 2008, Du Toit, 2003, Kutilek, 1979). In the wet season, assemblages close to water comprise largely grazers across the body size spectrum, particularly in more open, short grass habitats, mixed feeders across the body size spectrum, with few large browsers. Further from water, assemblages comprise less grazers and more browsers across the body size spectrum, particularly in denser habitat of increased grass height. In the dry season, assemblages close to water comprise largely of medium grazers, which occupy open habitat of short grass height, and mega- mixed feeders. As the distance from water increases, assemblage composition includes more small mixed feeders, browsers and large grazers, particularly in denser habitat of increased grass height.

Furthest from water, assemblages comprise largely of large grazers and browsers, particularly in denser habitat of increased grass height, megagrazers at short grass height, and mega- mixed feeders.

Conclusion

Our results supported trends across body size classes and feeding types which have previously been described. However, herbivore studies have typically looked at aspects of the effects of environmental attributes on herbivores, whereas our study has tested a combination of aspects across scales and seasons, on an herbivore assemblage which differs in functional traits. The results of this study showed that water availability and forage quality and quantity largely alter the composition of the assemblage, particularly in the grazer and mixed feeder guild. The means utilised to test predation effects were insufficient to explore the relationship across functional types, indicating that broad-scale camera trap surveys, in our case, may not have been an effective tool in this regard.

The use of distance from water and grass regrowth measurements to reflect grazer biomass warrants more investigation at a less coarse grain, especially in areas further from water and which experience less grazing pressure. Finally, the models developed in this study are a comprehensive analysis of a wide spectrum of body sizes and feeding types across a broad environmental gradient. The detection and confirmation of previously described trends indicates that the use of environmental attributes in GLMs may be a useful means to predict herbivore presence across seasons at a landscape scale.

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APPENDICES

Appendix A: AICc value comparisons for global and final generalised linear models by functional types by binomial data. Final models are the product of the global model with the lowest AICc value, following the removal of variables which had large standard errors including 0.

	Component models:	AICc	Term Codes:
Grazers – Global Model	1/2/3/4/5/6/7/8/10	808.00	Burnt: 1; Dist:2; disttrees:3; grassbiomass:4; season 5; burnt:Dist:6; burnt:season:7; Dist;disttrees:8; Dist;grassbiomass:9; Dist:season:10
	1/2/3/4/5/6/7/8/9/10	809.79	
	1/2/3/4/5/7/8/10	809.82	
Grazers – Final Model	5/2/1/4	907.14	
Browsers-Global Model	1/2/3/4/6/7/9/10/11/14/15	1037.90	Access:1; Burnt:2; coefvarObst:3; Dist:4; disttrees:5; Pred:6; season:7; access:Dist:8; burnt:Dist:9; coefvarObst:Dist:10; coefvarObst:season:11; Dist:disttrees:12; Dist:Pred:13; Dist:season:14; Pred:season:15
	1/2/3/4/6/7/10/11/14/15	1039.13	
	1/2/3/4/6/7/9/10/11/13/14/15	1039.31	
Browsers- Final Model	4/7/9/10/11	1047.11	
Mixed Feeders – Global Model	2/3/5/6/7/8/9/10/11/12/14/15	981.72	Burnt:1; coefvargrassb:2; Dist:3; disttrees:4; grassbiomass:5; grassheight:6; season:7; coefvargrassb:Dist:8; coefvargrassb:season:9; Dist:grassbiomass:10; Dist:grassheight:11; Dist:season:12; grassbiomass:season:13; grassheight:season:14; Dist:grassheight:season:15
	2/3/5/6/7/8/9/12/13/14	982.11	
	2/3/5/6/7/8/9/10/12/13/14	982.18	
Mixed Feeders – Final Model	1/3/10	1031.24	
Small-Medium – Global Model	1/2/3/4/5/6/7/8/9/10/11/13/14	1033.50	Burnt:1; coefvargrassb:2; Dist:3; disttrees:4; grassheight:5; Pred:6; season:7; burnt:Dist:8; coefvargrassb:Dist:9; coefvargrassb:season:10; Dist:disttrees:11; Dist:Pred:12; Dist:season:13; grassheight:season:14
	3/4/5/6/7/11/14	1034.20	
	1/2/3/4/5/6/7/8/9/10/11	1034.44	
Small-Medium – Final Model	5/3/1	1085.68	
Medium – Global Model	1/2/3/4/6/7/8/9/10/11/12/14	917.08	Burnt:1; coefvargrassb:2; coefvarObst:3; Dist:4; grassbiomass:5; grassheight:6; season:7; burnt:Dist:8; coefvargrassb:Dist:9; coefvarObst:Dist:10; Dist:grassheight:11; Dist:season:12; grassbiomass:season:13; grassheight:season:14
	1/2/3/4/5/6/7/10/11/12/13/14	918.00	
	1/2/3/4/6/7/8/9/10/12/14	918.23	
Medium – Final Model	4/8/10	943.43	
Medium Large – Global Model	1/2/3/4/5/7/8/9/10/12/14/15	893.31	Burnt:1; coefvargrassb:2; Dist:3; disttrees:4; grassheight:5; Pred:6; season:7; burnt:Dist:8; burnt:season:9; coefvargrassb:Dist:10; coefvargrassb:season:11; Dist:disttrees:12; Dist:grassheight:13; Dist:season:14; grassheight:season:15
	1/2/3/4/5/7/8/9/10/11/12/14/15	893.33	
	1/2/3/4/5/6/7/8/9/10/11/12/13/14/15	893.72	
Medium Large – Final Model	14/12/8/9/15	911.83	
Megaherbivores – Global Model	3/5/6/9/10/12	980.87	Burnt:1; coefvargrassb:2; Dist:3; disttrees:4; grassheight:5; season:6; burnt:Dist:7; burnt:season:8; Dist:grassheight:9; Dist:season:10; disttrees:season11; grassheight:season:12
	1/3/5/6/9/10/12	981.52	
	1/3/5/6/8/9/10/12	981.80	
Megaherbivores – Final Model	10/9	986.35	

Appendix B: AICc value comparisons for global and final generalised linear models by functional types for biomass data. Final models are the product of the global model with the lowest AICc value, following the removal of variables which had large standard errors including 0.

	Component models:	AICc	Term Codes:
Grazers – Global Model	2/3/4/5/8	13352.37	Burnt: 1; Dist:2; disttrees:3; grassbiomass:4; season 5; Dist:distrees:6; Dist:grassbiomass:7; Dist:season:8; grassbiomass:season:9
	2/3/4/5/7/8	13353.53	
	2/3/4/5/6/8	13353.53	
Grazers – Final Model	8/7	13361.28	
Browsers-Global Model	2/3/4/5/8	11293.77	Access:1; coefvarObst:2; Dist:3; disttrees:4; season:5; coefvarObst:Dist:6; Dist:disttrees:7; disttrees:season:8; Dist:season:9; Dist:burnt:10; coefvarObst:season:11
	1/3/4/5/8	11294.27	
	3/4/5/7/8	11294.31	
Browsers- Final Model	9/10/6/11	11301.33	
Mixed Feeders – Global Model	4/7	14600.95	Burnt:1; coefvargrassb:2; Dist:3; disttrees:4; grassbiomass:5; grassheight:6; season:7; Dist:grassbiomass:8; Dist:season:9; grassbiomass:season:10; Dist:burnt:11
	1/3/4/5/7/8/9/10	14601.37	
	1/4/7	14601.46	
Mixed Feeders – Final Model	11/9/4	14605.09	
Small-Medium – Global Model	3/4/5/9/10	10194.59	Burnt:1; coefvargrassb:2; Dist:3; disttrees:4; grassheight:5; season:6; coefvargrassb:Dist:7; coefvargrassb:season:8; Dist:disttrees:9; Dist:grassheight:10; Dist:season:11; grassheight:season:12; coefvarObst:12
	3/4/5/6/9/10	10195.41	
	3/4/5/6/10/11/12	10195.43	
Small-Medium – Final Model	3/6/12/4	10205.92	
Medium – Global Model	2/3/4/6/7/8/9/10/13/14	10747.97	Burnt:1; coefvargrassb:2; coefvarObst:3; Dist:4; grassbiomass:5; grassheight:6; season:7; coefvargrassb:Dist:8; coefvargrassb:season:9; coefvarObst:Dist:10; Dist:grassbiomass:11; Dist:grassheight:12; Dist:season:13; grassheight:season:14; Dist:burnt:15
	2/3/4/5/6/7/8/10/13/14	10748.14	
	2/3/4/6/7/8/10/13/14	10748.35	
Medium – Final Model	15/13/10	10785.06	
Medium Large – Global Model	2/3/4/6/7/9/10/11/12	12502.33	Burnt:1; coefvargrassb:2; Dist:3; disttrees:4; grassheight:5; Pred:6; season:7; burnt:Dist:8; coefvargrassb:Dist:9; coefvargrassb:season:10; Dist:disttrees:11; Dist:Pred:12; Dist:season:13; season:burnt:14; season:grassheight:15
	2/3/4/7/9/10/11	12502.57	
	2/3/4/6/7/9/10/11	12503.86	
Medium Large – Final Model	13/11/8/14/15	12512.63	
Megaherbivores – Global Model	4/6/7	14600.62	Burnt:1; coefvargrassb:2; Dist:3; disttrees:4; grassheight:5; season:6; burnt:Dist:7; burnt:season:8; Dist:grassheight:9; Dist:season:10; disttrees:season11; grassheight:season:12; Dist:grassheight:13
	3/4/6/7	14601.03	
	4/5/6/7	14601.56	
Megaherbivores – Final Model	10/13	986.35	

Appendix C: Results from the final generalised linear model selected for each functional type – binomial data.

	Covariate	Estimate	Std Error	Relative weight of variable Pr(> z)
Grazers	(Intercept)	8.06	1.01	< 0.001
	seasonLateDry	2.18	0.54	< 0.001
	seasonLateWet	-0.76	0.54	0.164
	Di st	-1.57	0.47	0.001
	burntYes	-3.11	0.64	< 0.001
	grassbi omass	-0.85	0.09	< 0.001
	seasonLateDry: Di st	-0.51	0.15	0.001
	seasonLateWet: Di st	-0.16	0.28	0.5624
	Di st: burntYes	0.87	0.20	< 0.001
	Di st: grassbi omass	0.17	0.04	0.001
Browsers	(Intercept)	-2.34	1.02	0.022
	Di st	1.70	0.43	< 0.001
	seasonLateDry	-1.48	0.91	0.102
	seasonLateWet	-5.60	0.98	< 0.001
	burntYes	-0.65	0.53	0.217
	coefvar0bst	0.02	0.01	0.014
	Di st: seasonLateDry	0.35	0.11	0.002
	Di st: seasonLateWet	0.22	0.12	0.069
	Di st: burntYes	-0.03	0.16	0.835
	Di st: coefvar0bst	-0.01	0.01	0.001
	seasonLateDry: coefvar0bst	0.01	0.01	0.704
seasonLateWet: coefvar0bst	0.04	0.01	< 0.001	
Mixed Feeders	(Intercept)	1.19	0.49	0.015
	Di st	0.25	0.19	0.201
	burntYes	-0.18	0.47	0.691
	grassbi omass	-0.04	0.05	0.381
	Di st: burntYes	-0.14	0.15	0.349
	Di st: grassbi omass	-0.04	0.01	0.028
Small-Medium	(Intercept)	0.96	0.17	< 0.001
	grasshei ght	-0.01	0.01	< 0.001
	Di st	-0.19	0.04	< 0.001
	burntYes	-0.01	0.16	< 0.001
Medium	(Intercept)	8.70	1.01	< 0.001
	Di st	-2.36	0.47	< 0.001
	burntYes	2.10	0.45	< 0.001
	coefvar0bst	-0.07	0.01	< 0.001
	Di st: burntYes	-0.47	0.12	1.0.001
	Di st: coefvar0bst	0.021	0.01	
Medium-Large	(Intercept)	0.17	1.05	0.865
	Di st	0.51	0.26	0.049
	seasonLateDry	-1.61	1.20	0.183
	seasonLateWet	-3.50	1.05	0.001
	di sttrees	0.06	0.00	<0.001
	burntYes	4.1	0.73	<0.001
	grasshei ght	-0.13	0.03	0.003
	Di st: seasonLateDry	0.05	0.17	0.751
	Di st: seasonLateWet	1.38	0.21	< 0.001
	Di st: di sttrees	-0.02	0.01	0.001
	Di st: burntYes	-0.95	0.19	< 0.001
	seasonLateDry: burntYes	-2.44	0.69	< 0.001
	seasonLateWet: burntYes	-4.38	0.60	< 0.001
	seasonLateDry: grasshei ght	0.11	0.04	30.006

	seasonLateWet: grassshei ght	0.12	0.03	0.001
Megaherbivore	(Intercept)	-0.23	0.26	0.377
	Di st	-0.24	0.08	0.003
	seasonLateDry	0.35	0.35	0.313
	seasonLateWet	0.65	0.38	0.087
	grassshei ght	-0.01	0.05	0.381
	Di st: seasonLateDry	-0.66	0.18	0.001
	Di st: seasonLateWet	-0.04	0.12	0.703
	Di st: grassshei ght	0.01	0.01	0.012

Appendix D: Results from the final generalised linear mixed model for each functional type – Biomass data.

	Covariate	Estimate	Std Error	Relative weight of variable Pr(> z)
Grazers	(Intercept)	1706.64	249.33	< 0.001
	seasonLateDry	510.29	157.85	0.001
	seasonLateWet	16.84	167.57	0.919
	Di st	-441.79	138.35	0.001
	grassbi omass	-155.68	25.06	< 0.001
	seasonLateDry: Di st	-156.94	56.16	0.005
	seasonLateWet: Di st	61.96	89.86	0.490
	Di st: grassbi omass	43.83	13.76	0.001
Browsers	(Intercept)	666.06	128.78	< 0.001
	Di st	-153.39	52.75	0.003
	seasonLateDry	-187.63	116.24	0.106
	seasonLateWet	-563.07	116.71	< 0.001
	burntYes	-95.45	69.35	0.169
	coefvarObst	-3.71	1.12	0.001
	Di st: seasonLateDry	17.40	14.67	0.236
	Di st: seasonLateWet	31.57	15.32	0.039
	Di st: burntYes	8.18	20.96	0.696
	Di st: coefvarObst	1.02	0.45	0.023
	seasonLateDry: coefvarObst	0.45	0.92	0.635
seasonLateWet: coefvarObst	3.75	0.94	< 0.001	
Mixed Feeders	(Intercept)	1227.61	482.74	0.011
	Di st	164.98	191.65	0.389
	burntYes	-926.44	469.27	0.048
	grassbi omass	-37.82	52.93	0.475
	Di st: burntYes	142.17	153.69	0.355
	Di st: grassbi omass	-29.43	18.97	0.121
	Small-Medium	(Intercept)	-29.39	46.12
Di st		-8.87	2.99	0.003
seasonLateDry		-24.57	12.89	0.057
seasonLateWet		13.58	11.08	0.22
coefvarObst		0.48	0.25	0.068
di sttrees		0.90	0.39	0.023
Medium		(Intercept)	874.79	81.61
	Di st	-225.35	37.96	< 0.001
	burntYes	99.39	44.58	0.025
	seasonLateDry	-113.18	30.53	0.001
	seasonLateWet	-14.78	29.74	0.619
	coefvarObst	-6.16	0.71	< 0.001
	Di st: burntYes	-36.18	14.58	0.013

	Di st: seasonLateDry	21.07	10.50	0.045
	Di st: seasonLateWet	17.36	11.08	0.117
	Di st: coefvar0bst	1.75	0.32	< 0.001
Medium-Large	(Intercept)	-381.23	257.57	0.133
	Di st	108.00	67.50	0.110
	seasonLateDry	507.43	264.72	0.055
	seasonLateWet	114.83	228.56	0.615
	di sttrees	11.42	1.98	< 0.001
	burntYes	378.08	154.80	0.014
	grasshei ght	-0.58	7.25	0.935
	Di st: seasonLateDry	-61.86	42.22	0.143
	Di st: seasonLateWet	39.41	48.26	0.414
	Di st: di sttrees	-2.66	1.38	0.054
	Di st: burntYes	-67.33	45.01	0.134
	seasonLateDry: burntYes	-452.77	174.19	0.009
	seasonLateWet: burntYes	-390.21	133.66	0.003
	seasonLateDry: grasshei ght	-5.24	7.87	0.505
seasonLateWet: grasshei ght	0.61	7.25	0.932	
Megaherbivore	(Intercept)	438.87	267.76	0.101
	Di st	-50.48	79.52	0.525
	seasonLateDry	315.20	340.69	0.355
	seasonLateWet	1250.18	396.38	0.001
	grasshei ght	-0.85	5.60	0.878
	Di st: seasonLateDry	-159.18	122.56	0.194
	Di st: seasonLateWet	-99.03	120.22	0.410
	Di st: grasshei ght	0.95	1.82	0.601