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Diversity of habitat use by large grazers: an interaction between body mass and digestive strategy

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Sipho (on the right), in 2004-2005 you supervised our field team and created a great team spirit in the SABRE team! Thanks also for calling out species dung during our 190 km transect walk (adding up to 25,000 dung piles) without openly stating my insanity. We had a great time during these walks! Good luck in your current position as a contract manager in the EKZN Wildlife Chromolaena project...

Abstract

Africa is characterized by unique and diverse assemblages of large mammalian savanna herbivores, but their populations are increasingly confined to protected areas. Recent studies suggest that management of these areas should promote high spatial heterogeneity to conserve a high diversity of large herbivore species. Spatial heterogeneity has been defined as habitat heterogeneity to explain how different-sized species partition resources on a landscape scale. Large species are expected to distribute more evenly over the landscape than smaller species, because their wider food quality tolerance allows them to use more diverse habitats. Where previous work addressed only browsers, we tested the robustness of this hypothesis for savanna grazers. Moreover, we hypothesize that digestive strategy influences the relation between body size and diversity of habitat use, because non-ruminants can tolerate a wider diet quality range than ruminants. We determined the spatial distribution and habitat preference of different-sized large grazers in Hluhluwe-iMfolozi Park, South Africa, by counting dung and determining habitat types on line transects distributed evenly over the park, for a total length of 190 km. Larger ruminant grazers were more evenly distributed over the landscape than smaller ruminants and the diversity of habitat use strongly increased with body mass. Moreover, larger species selected a higher proportion of poor quality habitat. In contrast, non-ruminant grazers were more evenly distributed than the ruminants and body mass neither influenced diversity of habitat use nor the use of high quality habitat. We conclude that the digestive strategy of large herbivores influences the relation between body mass and the diversity of selected habitats but that this should be further explored for more species and reserves.

Introduction

Africa accommodates the most species rich and abundant assemblages of large mammalian herbivore species around the world from the horn of Africa in the north, through the Serengeti plains, to the savanna woodlands of southern Africa (Prins and Olff 1998, Olff et al. 2002). These diverse communities have a large impact on the ecosystems they inhabit (McNaughton 1993, Hobbs 1996, Detling 1998) and play an important socio-economic role (Gordon et al. 2004). As in other parts of the world, African herbivores become increasingly confined to protected areas (Newmark 1996) through growing human population pressures and land use change (Cincotta et al. 2000). If we want to protect the remaining hotspots of large herbivore diversity we need to understand what determines the distribution of these hotspots (Olff et al. 2002).

Many studies have tried to understand the observed diversity patterns of large African herbivores by investigating coexistence mechanisms. Though other mechanism have been put forward (Sinclair 1985) most hypotheses explained coexistence by proposing how species partition resources (Vesey-Fitzgerald 1960, Bell 1970, Jarman 1974, Du Toit 1990). Early work in the 1960s and 70s started the discussion that larger herbivore species can tolerate a lower quality diet (higher fiber content) than smaller species based on the allometry of metabolic rate and gut capacity (Bell 1971, Geist 1974, Jarman 1974). This led to the now generally accepted hypothesis that variation in resource quality and quantity allows herbivores of different body weight to coexist and hence might lead to observed herbivore diversity patterns (Coe 1983, Gordon and Illius 1996, Belovsky 1997, Prins and Olff 1998, Ritchie and Olff 1999, Wilmshurst et al. 2000, Arsenault and Owen-Smith 2002, Olff et al. 2002, Crowsigt and Olff in press).

Based on this hypothesis Du Toit and Owen-Smith (1989) explore how body mass differences influence the way in which African savanna herbivores partition resources by selecting different habitats. They hypothesized that the wider food quality tolerance of larger species allows them to use a higher diversity of habitats, including habitats that are of too low quality for the smaller species. As a result larger species are more evenly distributed over the landscape than smaller species. This provides a mechanism through which spatially heterogeneous systems, i.e. systems with high habitat diversity, can support a higher diversity of different-sized herbivore species (see also Du Toit and Cumming 1999, Ritchie and Olff 1999, Olff and Ritchie 2001). Several other studies explained African herbivore coexistence through habitat partitioning (e.g. Hirst 1975, Dekker et al. 1996, Perrin and Brereton 1999, Oindo et al. 2003), but most of these studies lack such a general underlying mechanism.

Such a general mechanism is relevant for testing the 'heterogeneity paradigm' that is more and more adopted in the management of grazing systems (Fuhlendorf and Engle 2001, Du Toit and Cumming 1999, Du Toit et al. 2003, Kroger and Rogers 2005). This paradigm implies that managers should promote

high spatial heterogeneity in savanna systems to maintain high herbivore species richness and abundance; especially in relatively small, fenced savanna reserves (Owen-Smith 2004). In these small reserves resource heterogeneity might compensate for reserve extent and possibilities to migrate over large distances (Owen-Smith 2004, Fryxell et al. 2005). The problem is that heterogeneity is often poorly defined. Du Toit and Owen-Smith (1989) define heterogeneity as habitat diversity, allowing empirical testing of the heterogeneity paradigm. However, until now such tests have been hardly performed. While Du Toit and Owen-Smith (1989) showed that diversity of habitat use of browsers increased with body mass, they did not actually define habitats in terms of resource quality. Therefore, the proposed relation between diversity of habitat use and habitat quality remains to be quantified. Moreover, they conclude that there is a general relationship between herbivore body mass and diversity of habitat use, but only tested this relationship for ruminant browsers.

Non-ruminants can use a wider range of diet quality than ruminants. In contrast to ruminants, non-ruminants compensate for a less efficient nutrient extraction with a faster throughput rate, allowing them to more efficiently process low forage quality. Moreover, the faster throughput rate of non-ruminants results in less energy losses from high quality food due to the effect of methanogenic bacteria (Clauss et al. 2003). The net result is that ruminants are most efficient in processing intermediate quality food, while non-ruminants do best at the extremes (Owen-Smith 1988, Hofmann 1989, Duncan et al. 1990, Illius and Gordon 1992, Van Wieren 1996, Clauss et al. 2003). Therefore, non-ruminants might 'act' larger than they are, and use a wider range of habitat quality than expected from their body mass. Following this argument, Illius and Gordon (1992) already hypothesized that competition of zebra with the much larger buffalo is more likely than with the similarly-sized wildebeest (see also Grange et al. 2004). We hypothesize that the influence of body mass on diversity of habitat use is less strong for non-ruminants, because their digestive system allows smaller species to compensate for lower quality diets. We tested this hypothesis for ruminant and non-ruminant grazers in Hluhluwe-iMfolozi Park, South Africa, looking at an effect of feeding guild as well as digestive strategy.

Methods

The study was performed in the Hluhluwe-iMfolozi Park; a 90,000 ha protected area in Kwazulu-Natal, South Africa. This reserve is situated in the southern African savanna biome and is characterized by high habitat heterogeneity, ranging from open grasslands and thickets to closed *Acacia* and broad-leaved woodlands (Whateley and Porter 1983, Owen-Smith 2004). This heterogeneity can be partly explained by strong gradients in altitude and mean annual rainfall in the park, ranging from 700 – 1000 mm rainfall per year in the hilly northern part of the reserve to 650 mm in the southern basin (Brooks and MacDonald 1983, Owen-Smith 2004).

From August to October 2004 we counted dung of all larger grazer species in the park on 24 line transects that varied between 4 and 11 km (8 km on average, see chapter 1 for more detail), with a total length of 190 km. Transects were evenly distributed over the reserve, covering all vegetation types and elevations (Fig. 1). The most southern end of the park was excluded from the study, due to regulatory restrictions on research in this part (wilderness concept). The transects were walked with a team of two well-trained observers that continuously counted the number of dung pellet groups per species on and within 1 meter on each side of the transect. The number of dung pellet groups per species was recorded per 5 meter plot on a transect. We recorded dung of the 6 most frequently observed grazer species consisting of 3 ruminant grazers (impala, blue wildebeest and African buffalo) and 3 non-ruminant grazers (common warthog, common zebra and white rhino). White rhino typically use territorial dung heaps (middens) that are scattered over the landscape in low density. Therefore, to get a good distribution estimate for this species we counted all white rhino middens that we could see from a transect, instead of within 1 meter of each side.

Table 1 - Description of habitat types that were recorded on the dung count transects.

Habitat type	Description
Grassland	Open grasslands existing of tall caespitose grasses (mostly <i>Themeda triandra</i>) with no or hardly any trees (< 5%).
Thicket	Areas covered by impenetrable woody vegetation (> 75% shrubs and/or trees).
Open woodland	All woodlands with separated tree canopies.
Closed woodland	All woodlands with overlapping or bordering tree canopies.
Riverine forest	Gallery forest bordering rivers characterized by <i>Ficus</i> species.
Gallery forest	Evergreen gallery forest characterized by tall trees of <i>Celtis africana</i> and <i>Harpephyllum caffrum</i> and no or hardly any grass layer.
Watercourses	Main watercourses that were not covered by forest.

Every 100 meters along a transect we recorded habitat type as the dominating type in a 500 meter radius around the recording point, classified in 7 types; grassland, thicket, open woodland, closed woodland, riverine forest, gallery forest and watercourses (Table 1). We measured grazer habitat quality independently from habitat type. Because direct quality measurements (e.g. plant nutrient concentrations) were too laborious and expensive to collect on this scale (we recorded habitat type for a total of 1960 points), we estimated habitat quality according to two classes; grazing lawn present (high resource quality) and grazing lawn absent (low resource quality). Grazing lawns generally offer higher resource quality than other grassland types in terms of relatively low leaf C/N ratio, high concentrations of other nutrients such as sodium as well as structural characteristics such as high leaf-stem ratio and leaf productivity (McNaughton 1979, Ruess et al. 1983, McNaughton 1984, chapter 3). Similar to the dung counts,

we recorded grazing lawn presence every 5 meter along the transect. We defined grazing lawn as present when lawn grass species dominated (> 75 %) a 5 meter plot and extended for several meters away on both sites of a transect (at least 5 meters). I.e. if lawn species only covered the transect it was not recorded as grazing lawn.

Data analysis

Species distributions

We made relative density maps using ARCGIS 9.0 (ESRI 2004) to visualize how the different species were distributed over the landscape. We overlaid the dung count data with a grid of 2.5 by 2.5 km cells and summed the number of dung pellet groups per species per grid cell (n) (Fig. 1). We then divided the sums per species (n_i) by the total number of meters that a grid cell was intersected by transects to get a density estimate (no. dung pellet groups per meter) for each grid cell. Finally we determined relative densities for each species by dividing the density per grid cell by the maximum density found per species. We only calculated relative density for grid cells that were intersected by minimally 500 meter transect.

To test our hypothesis that large ruminants are more evenly distributed over the landscape than smaller species we determined Moran's I (Moran 1948) values for the spatial distribution of densities of all 6 grazer species. Moran's I is a measure of autocorrelation and is estimated as

$$I = \frac{N \sum_i \sum_j W_{i,j} (X_i - \bar{X})(X_j - \bar{X})}{\left(\sum_i \sum_j W_{i,j} \right) \sum_i (X_i - \bar{X})^2}$$

where N is the number of locations, X_i is the value of X on location i , X_j the value of X on a different location j and \bar{X} is the overall mean of X (in our case absolute density). $W_{i,j}$ is the inverse Euclidian distance between two locations i and j , and weighs the correlation between the locations so that locations that are further apart are less dependent. The index ranges between -1 and 1, from a highly dispersed (-1) to a highly clustered distribution (+1). According to our hypothesis smaller ruminants should be more clustered than larger ruminants, i.e. Moran's I should decrease with ruminant body mass. Furthermore, we expect non-ruminants to generally have a lower Moran's I than the ruminant grazers and I should not clearly depend on body mass. We used a Z -test to test whether Moran's I values were significantly different from a random distribution. Moran's I and Z scores were calculated with ARCGIS 9.0 (ESRI 2004).

Habitat selection

We used each recorded 5 meter plot as our basic unit to estimate habitat selection. Dung counts and lawn presence were recorded at this resolution, but habitat types were only recorded every 100 meters. Therefore, we assumed that the habitat type remained the same for the 5 meter units during the 100 meters following each habitat type recording. This assumption allowed us to classify all 7

habitats as high (with grazing lawn) or low (without grazing lawn) resource quality habitats, resulting in a total of 12 habitat classes for calculating habitat selection indices (a low and high quality type of each habitat class, gallery forest and watercourses had no grass layer and therefore only represented low quality habitat). As a measure of habitat selection we calculated Manly's standardized selection ratios (Manly et al. 2002). We firstly calculated resource selection functions as the proportion of available habitat units (5 meter plots) of habitat i that was selected by species s . $W_{i,s}$ is estimated as:

$$\hat{w}_{i,s} = o_{i,s} / \pi_i$$

where $o_{i,s}$ is the proportion of sampled dung pellet groups for species s that was found in units of habitat i . π_i is the proportion of available habitat units of all sampled habitat units that represented habitat i . We standardized the selection functions according to:

$$B_{i,s} = \hat{w}_{i,s} / \left(\sum_{i=1}^{i=12} \hat{w}_{i,s} \right)$$

where $B_{i,s}$ is the standardized selection ratio for species s and habitat type i which can be interpret as the probability that species s selects habitat i if all habitats would be equally available.

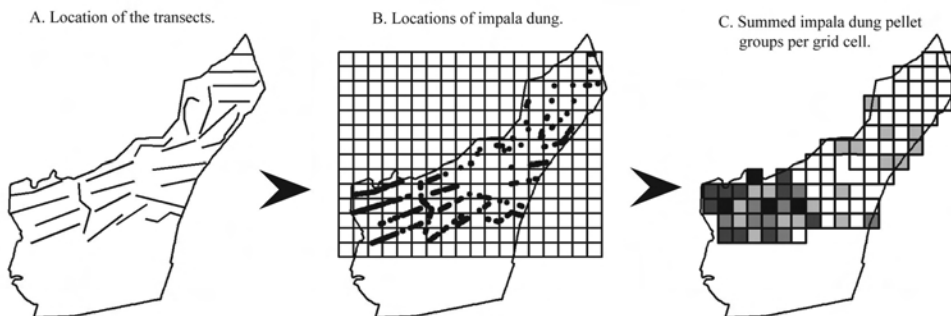


Figure 1 - Process of joining a 2.5 by 2.5 km grid with the dung count point data using ArcMap 9.0 (ESRI 2004). A. Outline of Hluhluwe-iMfolozi Park showing the position of the 24 transects. B. Locations where we found dung of a species (in this case impala), overlaid with a grid of 2.5 by 2.5 km cells. C. Result of the join of the overlay grid with the dung count data for grid cells that were intersected by at least 500 meter transect. The result is the number of impala dung pellet groups summed per grid cell. The darker the higher the abundance of impala dung.

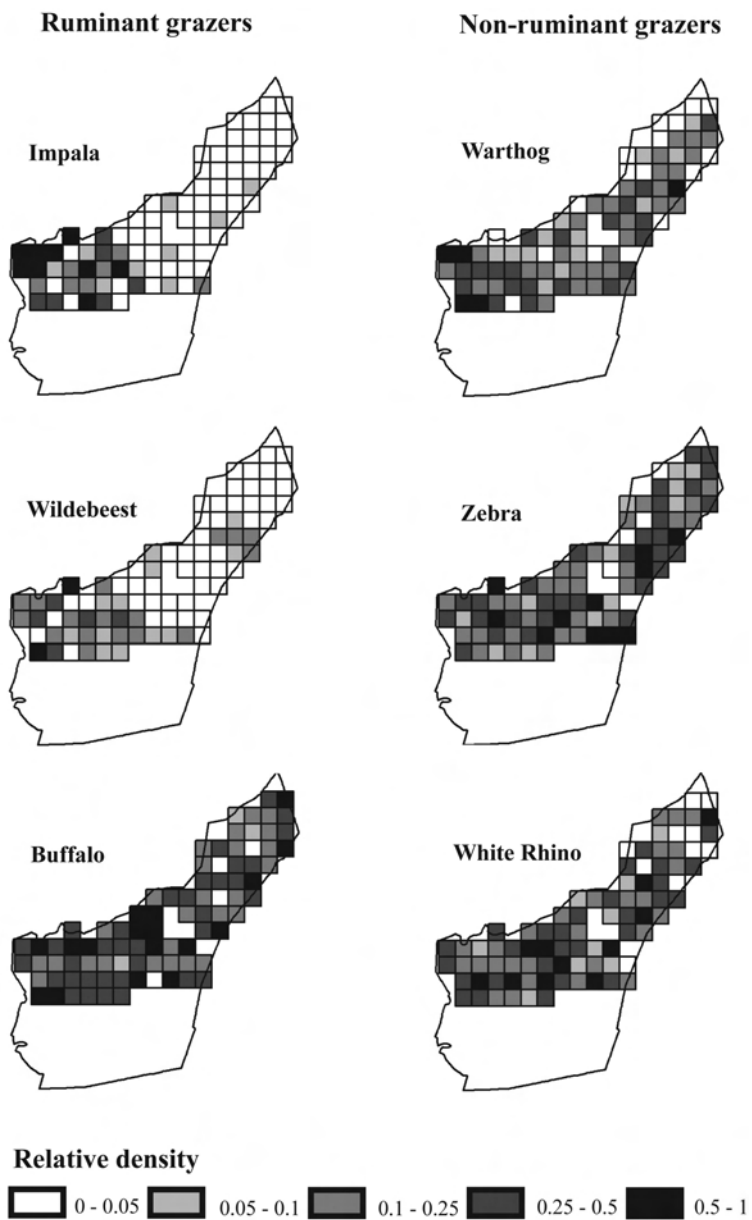


Figure 2 - Distribution of ruminant and non-ruminant grazers in Hluhluwe-iMfolozi Park. Distribution is expressed as relative densities (proportion of maximum observed density) of dung pellet groups for 6 grazer species in 2.5 by 2.5 km grid cells.

Per species we calculated the diversity of habitat use as Shannon-Wiener diversity index (Pielou 1975, Du Toit and Owen-Smith 1989) using the standardized selection ratios as proportions of habitat use:

$$H' = -\sum_{i=1}^{i=12} B_i \log B_i$$

Finally, per species we summed the standardized selection indices B_i of all habitats that were covered with grazing lawn to get an idea of the proportion of high quality habitat that was selected by each species.

Grazing lawn abundance and grazer density

In the previous analyses habitat preference and species density were not directly related. Therefore we analyzed how the relative densities of the 6 species depended on the proportion of grazing lawn per grid cell using linear regression (for $N = 84$ grid cells). We determined the proportion grazing lawn per grid cell as the proportion of transect 5 meter plots in the grid cell that was covered with grazing lawn.

Results

Species distributions

There were clear differences between the landscape distributions of the 6 grazer species (Fig. 2). Impala were strongly concentrated in the south-western part of the park. The intermediate-sized wildebeest were slightly more dispersed over the landscape, with concentrations in the south-west, similar to impala and similar high abundance locally in the north-east. Relative densities for the largest ruminant, buffalo, and the non-ruminants were much more evenly distributed over the landscape, with approximate equal abundances found in most places. This is also illustrated through the rank-abundance distributions, which became more strongly right-skewed for the smaller ruminants, while this distribution did not clearly change with body mass for the non-ruminants (Fig. 3).

Moran's I values confirmed this conclusion. All three ruminant grazers were significantly clustered in the landscape ($P < 0.01$) but Moran's I strongly declined with body mass for the ruminant grazers (Fig. 4), indicating that smaller ruminant grazers are more clustered in the landscape than larger grazers. Moran's I was not as clearly related to body mass for the non-ruminant grazers (Fig. 4). Moreover, distribution of zebra and white rhino was not significantly different from a random distribution. Warthog distribution was clustered ($P < 0.01$) but much less than the ruminant grazer with comparable body mass, impala.

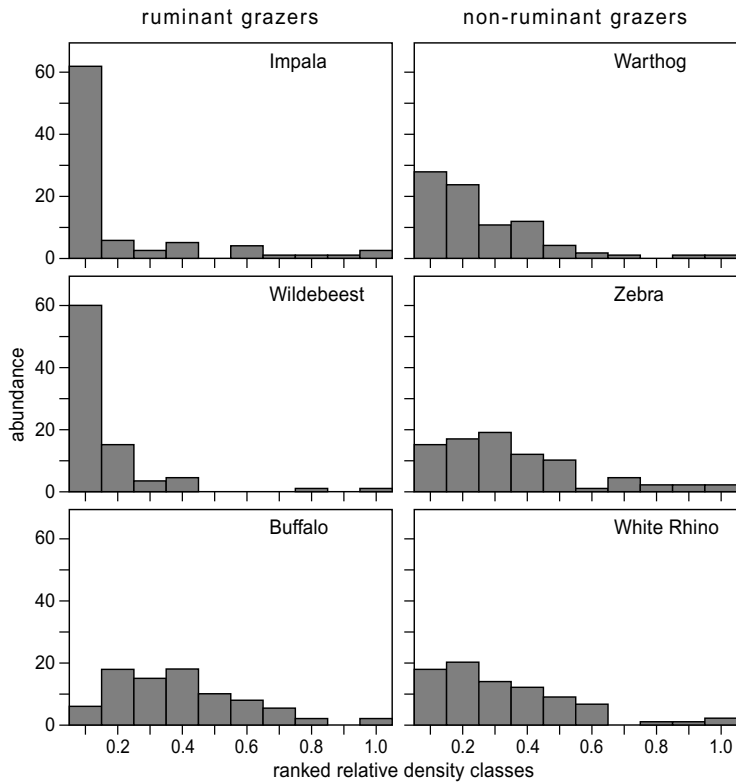


Figure 3 - Rank – abundance plots of the relative densities that are displayed in figure 2. Bars show the number of 2.5 by 2.5 km grid cells with relative densities falling within the classes that are defined on the x-axis.

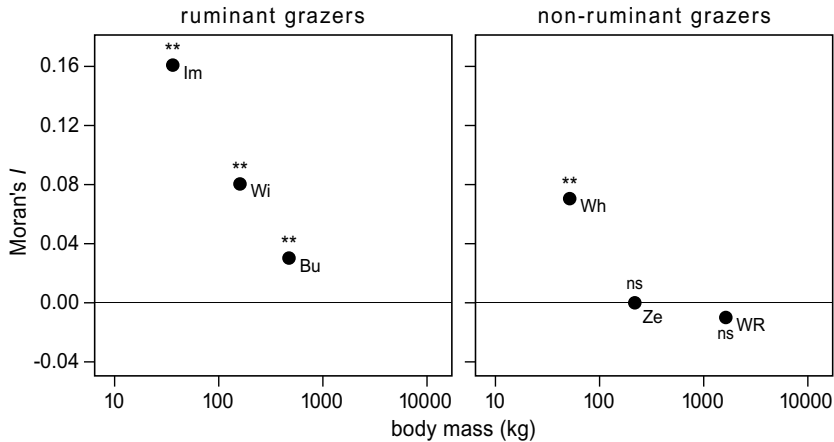


Figure 4 - Moran's I values for ruminant (left) and non-ruminant (right) grazers against their body mass. Ruminant grazers; IM (impala) $I = 0.16$, $Z = 12.4$, WI (wildebeest) $I = 0.08$, $Z = 7.4$, BU (buffalo) $I = 0.03$, $Z = 3.1$. Non-ruminant grazers; WH (warthog) $I = 0.07$, $Z = 6.0$, ZE (zebra) $I = 0.00$, $Z = 1.5$, WR (white rhino) $I = -0.01$, $Z = 0.8$. NS indicates that distribution of the species is not significantly different from a random distribution, ** indicates that densities of the species were spatially autocorrelated and significantly different from a random distribution with $P < 0.01$ (in our case clustered because for all species $I > 0$). Body mass represents the average over male and female body mass as given by Owen-Smith (1988).

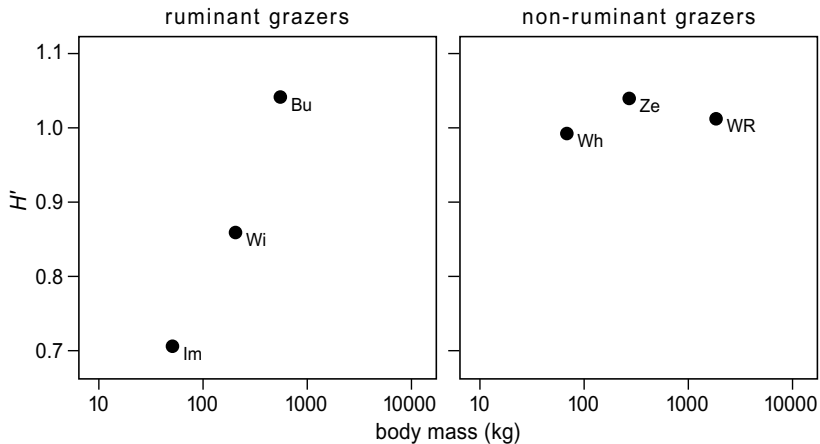


Figure 5 - Shannon-Wiener diversity index for selected habitat by ruminant (left) and non-ruminant (right) grazers against their body mass. Im: impala, Wi: wildebeest, Bu: buffalo, Wh: warthog, Ze: zebra, and WR: white rhino. Body mass represents the average over male and female body mass as given by Owen-Smith (1988).

Habitat selection

Diversity of habitat use strongly increased with increasing body mass for the ruminant grazers (Fig. 5). The Shannon-Wiener index of diversity (H') of habitats used increased from 0.7 for impala to 1.05 for buffalo. All non-ruminant grazers had a very diverse habitat use comparable to the largest ruminant grazer, the buffalo ($H' > 0.99$ for all three species) and diversity of habitat use did not increase with body mass (Fig. 5). Warthog and zebra had a much higher diversity of habitat use than expected from their body mass. The increase in diversity of habitat use with increasing body mass of the ruminant grazers coincided with a decreased selection of habitat that was covered by grazing lawn (Fig. 6). This decrease was not apparent for the non-ruminant grazers (Fig. 6) and especially the selection of lawn covered habitat by warthog and zebra was not as strong as expected from their body mass. The total number of dung pellet groups that we recorded per species was 6709 (buffalo), 2571 (wildebeest) and 4361 (impala) for the ruminants and 735 (white rhino), 2362 (zebra) and 1914 (warthog) for the non-ruminant grazers.

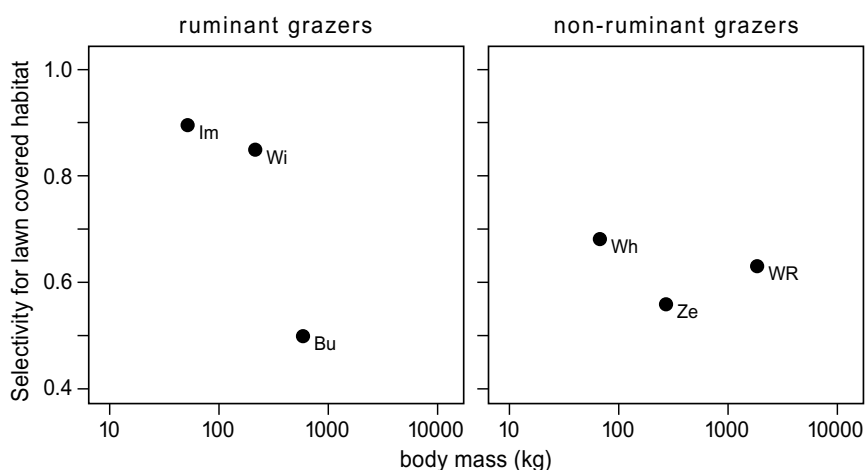


Figure 6 - Summed habitat selection indices (B_i) of habitats that were covered by grazing lawn against the body mass of the ruminant (left) and non-ruminant (right) grazers. Im: impala, Wi: wildebeest, Bu: buffalo, Wh: warthog, Ze: zebra, and WR: white rhino. Body mass represents the average over male and female body mass as given by Owen-Smith (1988).

Grazing lawn abundance and grazer density

The densities of the species that were most clustered in the landscape (impala, wildebeest and warthog, Fig. 4) increased with grazing lawn abundance in a grid cell (impala: $R^2 = 0.32$, $F_{1, 83} = 38.28$, $P < 0.01$; wildebeest: $R^2 = 0.30$, $F_{1, 83} = 35.73$, $P < 0.01$; warthog: $R^2 = 0.26$, $F_{1, 83} = 29.28$, $P < 0.01$). White rhino density also increased with proportion of grazing lawn, but the explained variation was

very low ($R^2 = 0.06$, $F_{1, 83} = 5.63$, $P = 0.02$). Zebra and buffalo density was not correlated with the abundance of grazing lawn in a grid cell ($R^2 = 0.03$ and 0.02 , $F_{1, 83} = 2.13$ and 1.24 respectively, $P > 0.05$). Figure 7 shows average relative density for all species per lawn abundance class and confirms the results from the linear regressions. It also confirms the results from the habitat selection indices that warthog and zebra select areas with low lawn cover, in contrast with impala and wildebeest.

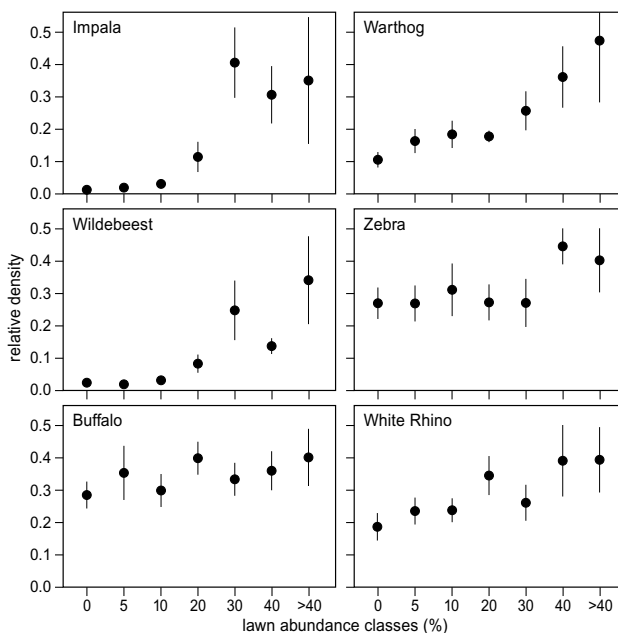


Figure 7 - Average relative density of 6 grazer species per lawn abundance class (0 % lawn cover in a grid cell, 1-5%, 6-10%, 11-20%, 21-30%, 31-40% and > 40% cover). Error bars represent the standard error around the mean.

Discussion

Larger ruminant grazers were more evenly distributed over the landscape than smaller ruminants (Fig. 2, 3 and 4). Moreover, the diversity of habitat use of ruminant grazers strongly increased with increasing body mass, as Du Toit and Owen-Smith (1989) showed for ruminant browsers. Our data supported the hypothesis that increased diversity of habitat use is related to a greater use of poor quality habitat (habitat without lawn cover) by larger species (Fig. 6 and 7). However, as hypothesized, the non-ruminant grazers deviated from this

relationship. Only the smallest non-ruminant, warthog, was significantly clustered in the landscape, but not as strongly as expected from its body mass (Fig. 4). Furthermore, body mass did not clearly influence diversity of habitat use or use of high quality habitat of the non-ruminant grazers. While first tested for browsers, the general applicability of the hypothesis of Du Toit and Owen-Smith (1989) seems to hold for ruminant grazers as well, but not for non-ruminant grazers. The smaller and intermediate-sized non-ruminants, warthog and zebra, seemed to 'act' larger and had a more diverse use of habitats than expected from their body mass. However, more species in different parks need to be explored before this can be definitely confirmed.

The increase in diversity of habitat use with body size that we observed for grazers was much higher than for the browsers in the study of Du Toit and Owen-Smith (1989). The diversity of habitats used by grazers in our study increased with 50% while body mass increased 10-fold. In contrast Du Toit and Owen-Smith (1989) found for browsers in Kruger NP that H' only increased with 20% while body mass increased 70-fold. The number of habitat classes defined by both studies was similar (12 in our study versus 14) and, therefore, does not explain the different increase in diversity with body mass. However, the relative availability of the different habitat types might be different in the study sites, Kruger NP and HiP. If some of the 14 habitat types are very dominant in Kruger NP and others are only sparsely available in a few locations, this would decrease the potential diversity of habitat that can be selected by species. Unfortunately, we do not have the data to test this. However, it emphasizes the importance of evaluating the relation between body mass and diversity of habitat use relative to the scale of heterogeneity of the study system. HiP is arguably a more heterogeneous system, where habitat types alternate at a finer scale than in Kruger NP and are available throughout the reserve. This makes it easier for species to choose among different habitat types. Future studies should, therefore, focus on investigating the relation between body mass and habitat selectivity across a range of reserves that differ in scale of habitat heterogeneity.

We defined habitat quality in terms of presence of grazing lawn. While lawns generally offer high resource quality, we realize that this is a fairly rough classification. To get a good idea about how diversity of habitat use is related to diet quality tolerance it is necessary to get a more continuous estimate of resource distribution. While sampling effort quickly limits the scale and resolution of classifying habitat quality with conventional techniques, new remote-sensing techniques (Mutanga 2004, Ferwerda et al. 2005) might make it possible to map habitat quality in detail on a large-scale in the near future. Such maps would make it easier to compare the role of variation in habitat resource quality with other habitat characteristics that can interact with quality to determine the distribution of large herbivores (see e.g. the large SE around the mean in Fig. 7).

Redfern et al. (2003) showed for Kruger NP that water availability can influence herbivore distribution on a landscape scale. Permanent water sources are,

however, widely available in HiP, and, therefore, water is not expected to limit grazer landscape distribution in HiP. Predation is another important factor that can influence herbivore distribution. Hopcraft et al. (2005) recently suggested that lions rather focus on areas with high prey catch ability than high prey abundance, explaining why herbivores avoid dense cover habitats (Sinclair 1985, Prins and Iason 1989). Larger herbivores, however, experience a lower predation pressure than smaller herbivores (Sinclair et al. 2003). This difference in predation pressure might explain why larger species use a wider range of habitats, because they can use habitats that are of too high risk for smaller species. Consequently, differences in predation pressure and habitat quality can cause the same body mass – herbivore distribution patterns. Both factors are, however, not necessarily convergent. Habitats can be of high quality, but too dense and therefore too risky for small ruminants to select. We need more empirical work to test how the interaction between habitat quality and predation risk influences large herbivore distributions.

We showed that for grazers the effect of body mass on diversity of habitat use depended on digestive strategy. In this study we classified grazers according to their digestive strategy as ruminants and non-ruminants, which is a fairly coarse classification. The digestive systems differ substantially among the non-ruminants in our study. Like all members of the order of odd-toed ungulates (Perissodactyla) zebra and rhino are hindgut-fermenters, while warthog, like the ruminants, belongs to the even-toed ungulates (Artiodactyla), which are all foregut fermenters. Of all members of the Artiodactyla suids, however, have very simple digestive systems with no rumination. We suggest that this allows them to use a wide range of food quality, comparable to the hind-gut fermenter, because they also benefit from a low retention time. Moreover, pigs have a relatively well-developed hindgut anatomy (caecum, colon), enabling them to handle relatively high fiber food (Leus and MacDonald 1997). Therefore, we classified them with the hindgut fermenters in terms of diet quality tolerance. Indeed, several members of this family, such as wild boar and bushpig, exhibit a very diverse diet, from high quality fruits to low quality grass (Leus and MacDonald 1997). However, studies that actually compare the digestive efficiency of wild suids with ruminants or hind-gut fermenters are lacking. In general, physiology is still poorly integrated into studies on herbivore resource ecology. The results of our study emphasize the importance of increasing our knowledge of physiology of wild ungulates and the impact on their ecology.

An effect of digestive strategy on the allometry of habitat selection, as suggested by our results, sheds an interesting light on recent developments regarding the allometry of home range size (Haskell et al. 2002, Jetz 2004, Carbone et al. 2005). These studies provide new mechanisms to explain observed home range – body size scaling. Based on differences in resource requirement and resource distribution they explain why trophic groups (e.g. herbivores versus carnivores) have different scaling exponents. None of these studies, however, include differences in digestive strategies within trophic levels. Our results suggest

that these models could be improved if differences in digestive physiology would be included, specifically for tropic groups such as herbivores with clear physiological differences.

Note that all species in our study are generally described as grazers, except for impala, which is often described as a mixed feeder eating grass as well as browse (e.g., Hofmann 1989). So the question is whether we rightfully included this species among the grazers in our study. Botha and Stock (2005) showed that impala in HiP are predominantly grazers, except during dry months when they increase the proportion of browse in their diet. However, even during these dry months grass still forms 60 % of the diet. Moreover, we showed that impala distribution was strongly related with the presence of grazing lawn (Fig. 7). These lawns are characterized by a high quality of the grass resource and not by an increased availability of high quality browse (they are actually relatively open areas with few shrubs). I.e. results indicated that impala landscape distribution in HiP is driven by the quality of the grass resource. Therefore, we believe that in HiP impala can be included in studies on the grazer guild, but this could be different in other reserves.

Concluding, our results suggest that diversity of habitat quality plays a role in resource partitioning on the landscape scale among different grazer species. In contrast with non-ruminants and large ruminants, the small to medium-sized ruminant grazers were concentrated in the areas with high grazing lawn abundance. Therefore, our results support the importance of considering spatial heterogeneity in management of savanna systems. Recent studies suggested that management decisions can significantly affect the proportion and spatial distribution of grazing lawns through managing fires (Archibald et al. 2005). However, more detailed mapping of resource quality on a large scale is essential to get a better insight in the relation between body mass and selection of habitat quality, because we showed that especially digestive strategy can significantly influence the strength of this relation. Moreover, wider empirical testing with more species and for other reserves, with different degree of habitat heterogeneity, is needed to support this conclusion.

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Large herbivore community structure and dynamics in different African savanna grassland types

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Sinenhlahla or S'neh, you've worked with us from 2003-2005 with great dedication. Your huge botanical species knowledge was vital to the project. I was very happy to hear that you got a job with Ezemvelo KZN Wildlife. I wish you all the best for the future...

Abstract

Studies on large grazer coexistence and diversity patterns have for long been dominated by ideas from east African systems. These systems are characterized by very large (square kilometers), homogeneous grasslands inhabited by a wide range of grazer species. These studies showed the role that spatial-temporal processes can play in structuring grazer assemblages, such as grazing succession during large-scale migrations. Many savanna reserves, especially in southern Africa, however are much smaller but still support high grazer species richness and abundance. These systems are often characterized by small-scale heterogeneity, where different grassland types alternate on a scale of only few 100 meters. In this study we explored if the spatial variation in resource quality and quantity offered by these different grassland types could promote diversity of African savanna grazers. We selected different grassland types (grazing lawn, bunch grassland and a mixed grassland) and measured average resource quality and quantity of these grasslands and visitation of grazer species over a period of more than 2 and half years. The lawn and mixed grassland had clearly higher N content in the leaves and higher contents of several essential minerals, especially Na, P and Cu. Grass standing biomass was highest in the bunch grassland, followed by the mixed site and lowest in the lawn grassland. Standing biomass in the bunch and mixed sites responded strongly to rainfall, while it remained fairly constant in the grazing lawn. We showed that the lawn and mixed sites were visited by twice as many species on a daily basis than the bunch grassland. The number of grazers that visited a site per day during the study period was 3 times higher in the grazing lawn than in the bunch grassland and even 4.5 times higher in the mixed site. After correcting for body mass these relative differences became smaller, and visitation was only 1.5 and 2 times higher in the lawn and mixed site respectively. Larger species, buffalo and white rhino, dominated the grazer assemblage in the bunch grassland, while the smaller wildebeest, impala and warthog dominated the assemblages of mixed and lawn site. Visitation was not stable, but varied over time. In the lawn and mixed site grazer visitation decreased after periods of low rainfall. The temporal dynamics of herbivore numbers in the bunch grassland were mainly driven by fire. Visitation in this grassland increased to the level of the mixed and lawn site during 2-3 months after a fire. Our results indicate that heterogeneity in grassland types might indeed promote grazer species richness and abundance. We discuss how our results support recent pleas that management should aim at maintaining and/or restoring grassland heterogeneity in tropical savannas.

Introduction

Large mammalian grazers are a characteristic part of many of the world's ecosystems, ranging from the Mongolian steppe to the vast plains of the Serengeti. Many studies have shown their diverse role in these grazing systems, influencing nutrient cycles (Holland and Detling 1990, McNaughton et al. 1997, Ritchie et al. 1998, Bakker et al. 2004), determining vegetation structure and composition (Cargill and Jefferies 1984, Augustine and McNaughton 1998, Olff and Ritchie 1998) and affecting numbers and diversity of other taxa (from birds to large carnivores: Milchunas et al. 1998, Carbone and Gittleman 2002). Besides this ecological role, the large grazers also are of great socio-economic importance (Gordon et al. 2004), directly as a protein source (Loibooki et al. 2002) and indirectly as a main driver of tourism activities (e.g., Barnes et al. 1999). However, together with the systems they live in, many of the large grazer populations are threatened by increasing human population pressure and economic activities (Cincotta et al. 2000, Balmford et al. 2001, Olff et al. 2002). To understand the impact of these threats we need insight in the mechanisms that are responsible for the spatial patterning of large grazer diversity and numbers.

Studies have shown that variation in food quality and quantity contributes to the coexistence of different grazer species (Du Toit and Owen-Smith 1989, Bugalho 1995, Gordon and Illius 1996, Belovsky 1997, Wilmshurst 2000, Cromsigt and Olff in press). Thus, spatial heterogeneity in food quality and quantity might promote large grazer diversity. This relation between spatial heterogeneity and diversity of large grazer species has been studied on different scales. On a continental to global scale variation in soil fertility and rainfall can reasonably predict large herbivore species richness patterns, through the impact of these factors on food plant quality and biomass (East 1984, Olff et al. 2002). On the scale of distribution of food patches (few square meters) studies showed that variation in size, spatial detail and quality of these food patches influences selectivity of grazer species differently and potentially determines large herbivore coexistence and diversity on a local scale (Hester et al. 1999, Cromsigt and Olff in press). There are far less studies that relate food heterogeneity to grazer species diversity at an intermediate scale (several 100 meters to a few kilometers). Studies that are available on this scale showed that habitat diversity promotes large mammal diversity (Fox and Fox 2000, Oindo et al. 2003), but often using a rough habitat classification, where grassland is classified as one habitat type. To explain large grazer diversity on this scale it is necessary to recognize different grassland types and quantify these types in terms of food quality and quantity.

Past studies have divided grasslands into (at least) two clear functional types; grasslands dominated by tall, bunch grass communities with a caespitose growth form and grasslands dominated by short, stoloniferous lawn grass species, i.e. grazing lawns (McNaughton 1984, Archibald et al. 2005). The existence of these grassland types has long been recognized, especially in African grazing systems.

Moreover, the value of grazing lawns for African grazer communities has also been increasingly stated (McNaughton 1984, Stalmans et al. 2001, Archibald et al. 2005). Grazing lawns have been described as areas where grazing promotes forage quality in terms of leaf N content (McNaughton 1979, Ruess et al. 1983, Coppock et al. 1983) and forage quantity in terms of primary production (McNaughton 1976, Hik and Jefferies 1990, Ruess et al. 1997). Compared with the lawns, the grass species that dominate bunch grasslands are of relatively low forage quality (low protein, high fiber content), but offer a high quantity of food, in terms of standing biomass. Fire, however, can temporarily increase the resource quality and quantity of grass in bunch grasslands (e.g. Van de Vijver, 1999). While many bunch grasslands burn easily and grazing lawns hardly burn, the relative effect of these burns on herbivore visitation of bunch grasslands compared with visitation of grazing lawns is not clear.

High spatial heterogeneity in grassland types might be essential for maintaining high species richness and abundance in relatively small reserves (Owen-Smith 2004). The grazing lawn concept in Africa has been dominated by studies from the Serengeti system describing fairly homogeneous systems with large lawns of kilometers by kilometers (McNaughton 1983). However, many other savanna systems, for example in Southern Africa, are characterized by a finer-scale heterogeneity, where lawn and bunch grasslands alternate on a scale of hundreds of meters. These same reserves are often characterized by high richness and abundance of relatively resident grazer species, compared with the migratory system in the Serengeti (Owen-Smith 2004).

The relation between grassland type heterogeneity and large grazer diversity patterns is not just relevant for our fundamental understanding. Recent studies showed that management actions can have huge impacts on this relation. Up to recently management authorities did not see grazing lawns as an essential part of the heterogeneous grazing landscape, but rather as over utilized patches (Stalmans et al. 2001). This paradigm is shifting (Mentis et al. 1989) and recent studies showed that management decisions, especially fire management, have a potentially large influence on grassland heterogeneity through its interaction with grazing (Fuhlendorf and Engle 2001, Archibald et al. 2005). Archibald et al (2005) showed that the type of fire regime potentially reduces the proportion of lawn grasslands in an area (see also Archibald and Bond 2003) and in this way might change grazer community composition and numbers.

Though the importance to manage small-scale spatial heterogeneity in grassland types for sustaining large grazer diversity is more and more emphasized (Owen-Smith 2004, Archibald et al. 2005), the grazer species richness and abundance on the different grassland types has not been well documented, especially outside east Africa. In this study we followed herbivore visitation and characterized resource quality and quantity in different grassland types to measure the relative importance of grazing lawns for large grazer species richness and

abundance compared to other grassland types in a heterogeneous savanna landscape.

Methods

The study was performed in Hluhluwe-iMfolozi Park (HiP), a relatively small (90,000 ha) but diverse protected area in Kwazulu-Natal, South Africa. This reserve is situated in the southern African savanna biome, with vegetation types ranging from open grasslands to closed *Acacia* and broad-leaved woodlands (Whateley and Porter 1983). The mean annual rainfall depends on altitude, ranging from 985 mm in the high altitude regions to 650 mm in the lower areas and mainly falls between October and March. Daily maximum temperatures range from 13 °C to 35 °C. The reserve is of strong conservation importance because it hosts a rich and complete set of indigenous large herbivores and carnivores. The park is characterized by a high heterogeneity in grassland types, where grasslands dominated by tall bunch grass (tussock forming) communities of *Sporobolus pyramidalis*, *Eragrostis curvula* and *Themeda triandra* are alternated by grasslands with short lawn-forming (stoloniferous) communities of *Digitaria longiflora*, *Urochloa mosambicensis*, *Dactyloctenium australe* and *Sporobolus nitens* at a scale of 100s of meters.

In the central area of this reserve we selected 3 open grassland sites, each several hectares in size. The sites were situated close to each other and we assume that grazer individuals could freely move between sites. The sites represented different grassland types; a bunch grassland, a grazing lawn and a mixed grassland. The mixed grassland was characterized by a highly heterogeneous grass layer, where relatively small (several square meters) grazing lawn patches were alternated by bunch grass patches in contrast with the much more homogenous lawn and bunch grasslands. We selected this mixed grassland because it is a dominant grassland type in the reserve and to evaluate to what extent visitation of these grasslands is comparable with homogeneous grazing lawns.

The burning regime in Hluhluwe-iMfolozi GR follows a prescribed burning practice where any area in the reserve is burnt once every 1-4 years with a median fire return period of 1.3 years (Archibald et al. 2005). Areas are burnt for three main reasons; against bush encroachment, to improve resource availability for the grazers and to control alien plants (Conway et al. 2001). Our sites burnt according to the park average, where the bunch grass site burnt twice, the mixed site burnt once and the lawn grass site did not burn during our three year observation period.

Grassland site characterization

In each grassland site we marked a 1 ha plot and laid out 10 fixed line transects, 10 meter apart, where we monitored vegetation height and grass functional type. Once a month we measured the height of the vegetation with a round disc of 46 cm width and a weight of approximately 460 grams. The disc, with a hole in the middle, was dropped along a pole with a height scale in cm. The height was measured to the nearest cm every meter along the 10 transects, resulting in

1000 measuring points per site per month. We determined the grass functional type every two months along the same fixed line transects. Every 4 meters along each transect we recorded whether the most dominant grass species was a bunch or a lawn grass species. This resulted in 250 grass functional type measurements per site per 2 months.

We clipped aboveground grass biomass in December 2002 (wet season 02/03), July 2003 (dry season 03) and January 2004 (wet season 03/04) to get an average food quality estimate for the three sites. We clipped two random samples along each of the fixed transects, resulting in 20 samples per site. We clipped all aboveground grass material in frames of 50 by 50 cm. Samples were dried and sorted into leaves, stems and dry matter to calculate leaf-stem ratio as a measure of structural quality for all three seasons. We then ground the leaves from the 2004 samples and analyzed these samples for organic N, C, the macro-elements Ca, Na, P, K and Mg and the trace elements Fe, Zn, Mn and Cu. N content was analyzed according to the macro-Kjeldahl digestion method, C content using the Automated Dumas dry combustion method while the minerals were extracted with HCL after which concentrations were determined calorimetrically for P and with atomic absorption for the other elements (Manson and Roberts 2000). In 2003 we also took soil samples to test the sites for difference in clay content. We took two samples along each side of the grassland plots with a 5 cm diameter soil core from the upper 10 cm of the soil, resulting in 8 samples per site. Samples were dried at 105 °C and after we ground the samples they were analyzed for % clay (particles <0.002 mm, Manson and Roberts 2000).

Grazer visitation

In each ha plot we created 5 fixed 1x5 meter sand beds around each side of the 1 ha plots to be able to count spoor of animals that visited the plots. To create these spoor plots we removed the top grass layer, creating a bed of a few cm deep. Thereafter, the bed was refilled with loamy sand from a local quarry. We checked the spoor plots for animal tracks once or twice a week between July 2002 and March 2005. Instead of counting individual tracks we counted individual track pathways to get a more realistic estimate of animal numbers. After each observation we wiped the spoor plots with a rake.

Data analysis

Grassland site characterization

Before further analysis, we calculated the proportion of each functional grass type per transect per site as an estimate for the cover of functional grass types per transect; i.e. if on 20 of the 25 sample points of a transect the dominant species was a lawn grass, lawn grass cover of that transect would be 80%. We averaged the resulting lawn and bunch cover per transect per site over all the sample dates (13 in total). In the same way, we averaged grass height per transect per site over all sampling dates (26 in total). Using a one-way analysis of variance, we tested for an

effect of site on grass height and % lawn cover, followed by Student-Newman-Keuls *a posteriori* contrasts (n = 10 for fixed transects).

We calculated the average monthly rainfall based on data from three weather stations that were closest to the sites to compare with trends in grass height over time.

Average overall visitation

Per sampling date we summed all spoor pathways per species per grassland site as a proxy for total number of individuals per species that visited the site since it was last checked for spoor. As a next step we calculated average daily visitation rates by dividing the number of individuals (spoor pathways) per species by the number of days since the site was last checked. We only used sampling dates where the number of days since last checked did not exceed 7 days. We finally summed visitation rates of all grazer species to come to an overall grazer daily visitation rate per site per sampling date.

We determined the number of species that visited each site per sampling date. We divided this number by the number of days since the site was last checked (again ≤ 7) to get an estimate of the number of species that visited a site per day for each sampling date.

We compared visitation rates as a measure of utilization of the different grassland types by the different grazer species. However, large species occur at lower densities but use more energy per individual than smaller species. Therefore, we should account for body mass differences if we want to infer potential utilization of different grassland types by different-sized grazers from the measured visitation rates. We transformed body mass to daily energy expenditure (DEE) as two times basal metabolic rate: $DEE = 2 * 70 * (\text{body mass})^{0.75} \text{ kCal day}^{-1}$ (Demment and Van Soest 1985, 1 kCal = 4.184 kJ). We used average species biomass as given by Owen-Smith (1988). We multiplied DEE per species with its average daily visitation rate ($\text{no. ha}^{-1} \text{ day}^{-1}$). By summing DEE over all species we come to an average DEE per grassland site for the grazer assemblage that visits the site on a certain day. We used this assemblage DEE as a measure of the potential utilization of a grassland type by this assemblage.

We tested how site affects daily grazer visitation rate, DEE and species richness with a repeated measurement analysis of variance (sampling date as repeated measurement). For this purpose we only used data of sampling dates when all sites were checked (total of 162 times). We tested whether sphericity could be assumed and corrected the degrees of freedom according to the Huynh-Feldt method (SPSS 12.0) if this was not the case. We used a Bonferroni *a posteriori* test to check for differences between sites.

DEE over time

We calculated the average DEE per month from August 2002 up to April 2005 for months with 3 or more sample dates. Using the average values per species we tested temporal correlation amongst visitation of species with a spearman rank correlation for each site separately.

Results

Grassland type characterization

During the 2.5 year study period the grass in the bunch grassland was on average more than twice as tall as in the lawn grassland, while the mixed grassland had an intermediate height (table 1). The proportion of stoloniferous short grass species was highest in the lawn grassland (table 1). We recorded no lawn species in the bunch grassland. The overall proportion of stoloniferous species was lower in the mixed grassland than in the lawn grassland and temporal variation of this proportion was much higher in the mixed site (see standard error and minimum/maximum values in table 1).

Table 1 - Summary statistics for the % of clay in the soil, the mean grass height and percentage lawn grass cover for three grassland types; bunch, mixed and lawn grassland. Different letters behind the means indicate a significant difference between treatments (Student-Newman-Keuls test after one-way analysis of variance). % Clay: $F_{2, 21} = 265.7$, $p < 0.01$; Grass height: $F_{2, 27} = 103.8$, $p < 0.01$; Lawn cover: $F_{2, 27} = 326.4$, $p < 0.01$.

	% Clay			Grass height (cm)			Lawn cover (%)		
	bunch	mixed	Lawn	bunch	mixed	lawn	bunch	mixed	lawn
Mean	51.8 ^b	22.6 ^a	25.0 ^a	14.4 ^c	9.3 ^b	6.4 ^a	0.03 ^a	62.4 ^b	73 ^c
Standard Error	1.11	0.75	1.07	0.60	0.23	0.24	0.03	3.4	1.58
Minimum	47	20	22	12.6	7.6	5.6	0	48	60.6
Maximum	57	26	30	18.8	10.2	7.8	0.31	75.7	77.5

The difference in temporal variation is also shown by the grass height development in the three grassland sites (Fig. 1). Grass height of the bunch grassland and the mixed site varied strongly over time responding to rainfall and fire events. The bunch grassland burnt the 31st of July 2002 and 5th of August 2004 and after these dates the height decreased to the level of the lawn grassland. Height remained short for 4-5 months and then increased strongly again as a response to high rainfall (Fig. 1). The mixed grassland burnt the 30th of August 2003 after which date the height was temporally shorter than in the lawn grassland. After 5 months the grass height increased again to intermediate level between lawn and bunch grassland in response to high rainfall. Compared with the bunch and mixed site, the grass height of the lawn grassland remained much more stable and did not strongly respond to variation in rainfall. During our study period the lawn grassland did not burn.

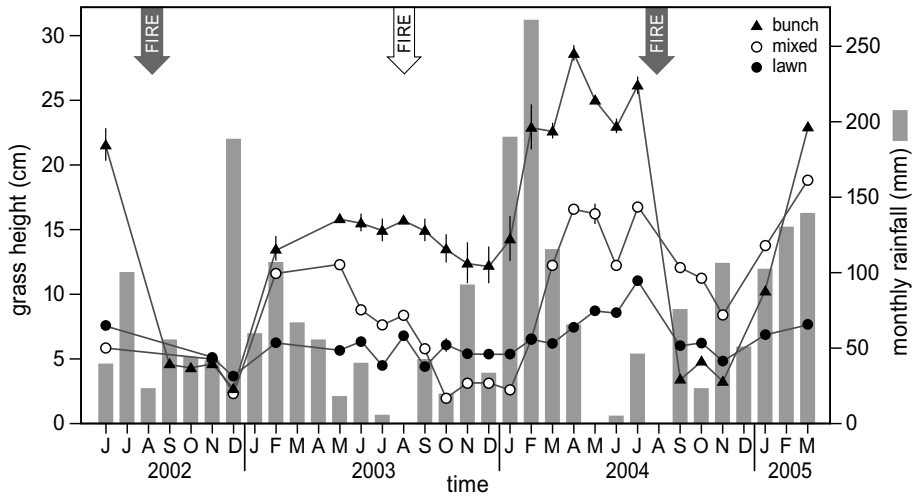


Figure 1 - Monthly averages for rainfall (gray bars in mm) and grass height (dashed lines in cm) in three grassland types; bunch (circles), mixed (triangles) and lawn (squares) grassland. The arrows show the timing of three fire events, two in the bunch grassland (solid arrows: 31 July 2002 and 5 August 2004) and one in the mixed grassland (open arrow: 30 August 2003). Error bars show standard error of the mean.

Leaf-stem ratio was higher in the bunch and mixed grassland than in the lawn grassland (Fig. 2, $F_{2, 164} = 8.4$, $P < 0.01$). In all sites the leaf-stem ratio decreased in the dry season to increase again in the next wet season (Fig. 2, $F_{2, 164} = 7.2$, $P < 0.01$). This decrease was caused by a reduced proportion of leaves in the dry season ($F_{2, 166} = 92.7$, $P < 0.01$), the proportion of stems remained the same between seasons ($F_{2, 166} = 0.82$, $P = 0.44$). The leaf N, Na, P, Cu and Zn content in the mixed and lawn grassland was higher than in the bunch grassland (table 2). In contrast the Ca, C and Mn content was higher in the bunch grassland than in the other two sites (table 2). Fe content was higher in the mixed site than in the other sites, while K content was highest in the lawn site (table 2).

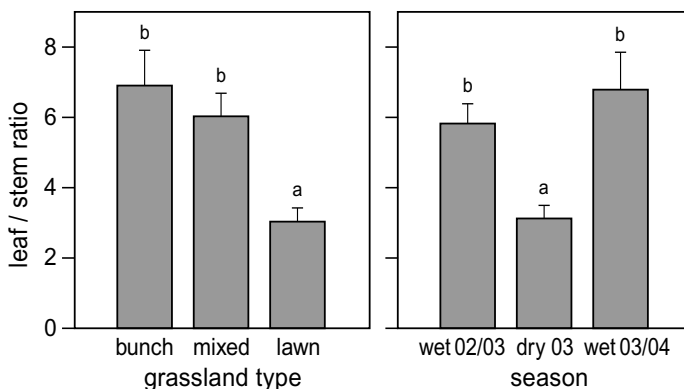


Figure 2 - Leaf-stem ratio (leaf dry weight over stem dry weight) per grassland site on the left-hand side and per season on the right-hand side. Wet02/03 was based on samples from December 2002, dry03 from samples from July 2003 and wet03/04 from samples from January 2004. Different letters indicate significant differences (Student-Newman-Keuls test after one-way analysis of variance). Error bars show standard error of the mean.

Table 2 - Summary statistics for leaf element concentration (in parts per million) in January 2004 samples from three different grassland types; bunch, mixed and lawn grassland. Different letters behind the means indicate a significant difference between treatments (Student-Newman-Keuls test after one-way analysis of variance). F -values and P -values of the ANOVA test are given for each element.

Element	Bunch	Mixed	Lawn	$F_{2,55}$	P
N (%)	0.91 ^a	1.80 ^b	1.88 ^b	99.4	< 0.01
Na (ppm)	1,085 ^a	5,643 ^b	5,666 ^b	67.9	< 0.01
P (%)	0.07 ^a	0.17 ^b	0.18 ^b	42.4	< 0.01
Cu (ppm)	2 ^a	6 ^b	5 ^b	27.3	< 0.01
K (%)	1.32 ^a	1.74 ^b	2.00 ^c	21.1	< 0.01
Ca (%)	0.32 ^b	0.23 ^a	0.25 ^a	17.2	< 0.01
Fe (ppm)	204 ^a	546 ^b	304 ^a	15.4	< 0.01
C (%)	43.79 ^b	42.55 ^a	42.91 ^a	5.6	< 0.01
Mn (ppm)	148 ^b	124 ^a	122 ^a	4.9	< 0.05
Zn (ppm)	21 ^a	37 ^b	33 ^b	4.3	< 0.05
Mg (%)	0.18 ^a	0.21 ^a	0.21 ^a	3.0	NS

Table 3 - Summary statistics for herbivore visitation rate, daily energy expenditure (DEE) and species richness for three different grassland types; bunch, mixed and lawn grassland. Different letters behind the mean values indicate a significant difference between treatments (Bonferroni a posteriori tests after a repeated measurement ANOVA with sampling date as the repeated measurement). Visitation rate: $F_{1,86,322} = 120.2$, $p < 0.01$; DEE: $F_{2,322} = 34.2$, $p < 0.01$; Species richness: $F_{1,90,322} = 195.1$, $p < 0.01$. The degrees of freedom for visitation rate and species richness were adjusted according to Greenhouse-Geisser correction because the assumption of sphericity was violated.

	Visitation rate (no. ha ⁻¹ day ⁻¹)			Daily energy expenditure (MJ ha ⁻¹ day ⁻¹)			Species richness (no. species ha ⁻¹ day ⁻¹)		
	Bunch	Mixed	Lawn	Bunch	Mixed	Lawn	Bunch	Mixed	Lawn
Mean	6.2 ^a	28.3 ^c	19.3 ^b	351.3 ^a	716.2 ^c	514.1 ^b	2.2 ^a	4.4 ^b	4.3 ^b
Standard Error	0.67	1.49	1.23	37.32	37.32	32.88	0.13	0.09	0.10
Minimum	0	1.1	0	0.0	12.7	0.0	0	1	0
Maximum	43	92.3	63.3	2432.4	3222.9	2108.6	6	6	6

Grazer visitation

The average daily visitation by large grazers was highest in the mixed grassland site, almost 5 times as high as in the bunch grassland (table 3). The visitation in the lawn grassland was somewhat lower than in the mixed site but still three times as high as in the bunch grassland (table 3). The differences in DEE between the sites showed the same pattern as the visitation rate (table 3), with the highest DEE in the mixed site and an intermediate DEE in the lawn grassland. However, the relative differences were smaller than for the visitation rate, indicating that larger species preferred the bunch grassland over the mixed and lawn site. The average number of species present on a day did not differ between mixed and lawn grassland, but was only half as high in the bunch grassland (table 3). The maximum number of species that visited a site on a certain day was as high in all sites (table 3).

Grazer species responded very differently to grassland type (Fig. 3, species \times grassland type: $F_{6.5, 1048.4} = 26.3$, $P < 0.01$). Wildebeest ($F_{2, 322} = 14.4$, $P < 0.01$), Warthog ($F_{1.7, 275.4} = 74.5$, $P < 0.01$) and Impala ($F_{1.8, 290.0} = 118.4$, $P < 0.01$) visited the lawn and mixed grassland more than the bunch grass site, where the two latter species strongly avoided the bunch grassland. Buffalo preferred the bunch grassland above the two other types ($F_{1.5, 243.2} = 20.4$, $P < 0.01$). We found significantly more Zebra in the lawn grassland ($F_{2, 322} = 7.1$, $P < 0.01$), while White Rhino was more abundant in the mixed grassland ($F_{1.9, 298.4} = 19.3$, $P < 0.01$). Impala was also more abundant in the mixed site than in the lawn grassland (Fig. 3).

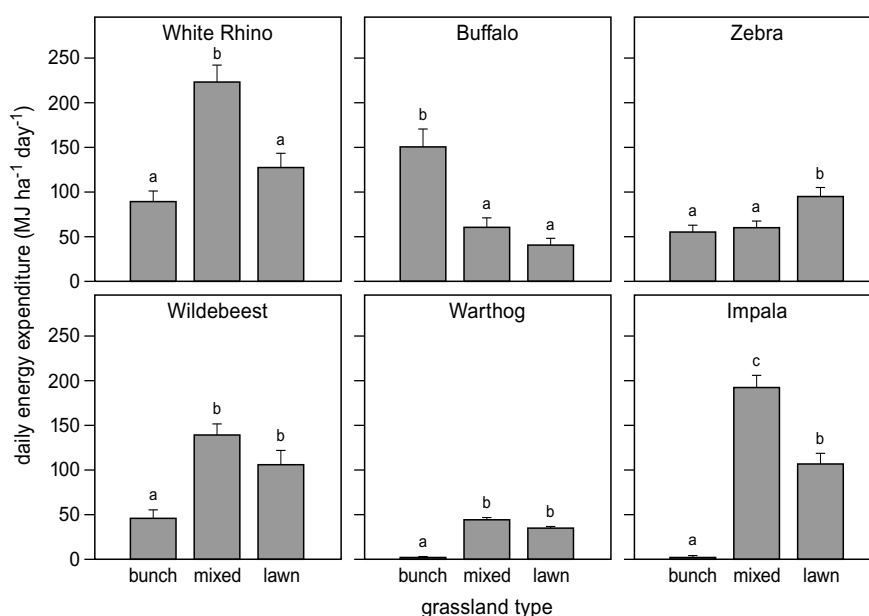


Figure 3 - Daily energy expenditure (DEE in MJ ha⁻¹ day⁻¹) for six grazer species in three grassland types; bunch, mixed and lawn grassland. Different letters indicate significant differences of DEE among grassland types for each species separately (Bonferroni test after a repeated measurement analysis of variance). Error bars show standard error of the mean.

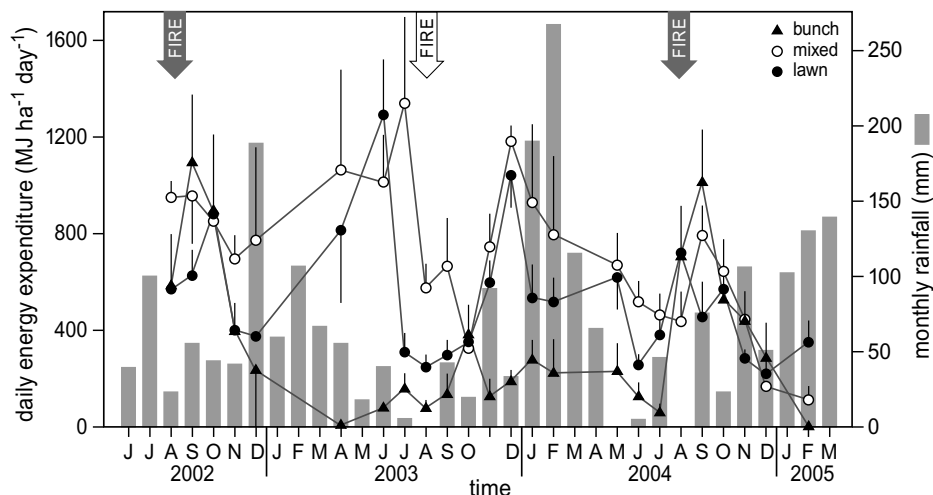


Figure 4 - Monthly averages of rainfall (grey bars in mm) and daily energy expenditure of the total large grazer assemblage ($\text{MJ ha}^{-1} \text{ day}^{-1}$) in three grassland types; bunch (circles), mixed (triangles) and lawn (squares) grassland. The arrows show the timing of three fire events, two in the bunch grassland (solid arrows: 31 July 2002 and 5 August 2004) and one in the mixed grassland (open arrow: 30 August 2003). Error bars show standard error of the mean.

Daily Energy Expenditure over time

Generally, the lawn dominated sites had a higher DEE over time than the bunch grassland (Fig. 4). DEE, however, was certainly not stable over time and seemed to decrease after periods of low rainfall (Fig. 4, especially July-September 2003). Fire events were responsible for the main temporal dynamics in the bunch grassland. After a fire DEE in the bunch grassland increased strongly towards the level in the mixed and lawn sites (Fig. 4). This post-burn effect lasted 2-3 months. The large to intermediate sized grazers were mainly responsible for this post-burn effect (Fig. 5). Buffalo, Wildebeest and White Rhino visitation to the bunch grassland increased strongly after the burns in 2002 as well as 2004 and was relatively low between these burn events. Zebra showed the same response, though its response in 2004 was less clear. There was no clear response of species to the burn in the mixed grassland.

We found no negative correlations between DEE per species over time. In contrast, DEE of several species was positively correlated over time in all three sites (table 4). Note that visitation of Wildebeest and Zebra and of Impala and Warthog were positively correlated in all sites.

Table 4 – Correlation matrix showing the spearman ρ correlation coefficients of combinations of daily energy expenditure (DEE) for 6 grazer species and three grassland types. The coefficients that are followed by an asterisk are significant (*: $P < 0.05$, **: $P < 0.01$).

Species	Grassland	Impala	White Rhino	Buffalo	Wildebeest	Zebra	Warthog
Impala	Bunch	1	0.27	0.36	0.34	0.13	0.47*
	Mixed	1	0.31	0.12	0.44*	0.11	0.58**
	Lawn	1	-0.01	0.44*	0.40	0.23	0.48*
White Rhino	Bunch	X	1	0.46*	0.71**	0.63	0.18
	Mixed	X	1	0.41*	0.31	0.15	0.10
	Lawn	X	1	0.29	-0.05	0.01	-0.05
Buffalo	Bunch	X	X	1	0.56**	0.40	0.16
	Mixed	X	X	1	0.12	0.19	0.15
	Lawn	X	X	1	-0.24	-0.11	0.21
Wildebeest	Bunch	X	X	X	1	0.58**	0.46*
	Mixed	X	X	X	1	0.47*	0.18
	Lawn	X	X	X	1	0.59**	0.30
Zebra	Bunch	X	X	X	X	1	0.14
	Mixed	X	X	X	X	1	0.09
	Lawn	X	X	X	X	1	-0.03
Warthog	Bunch	X	X	X	X	X	1
	Mixed	X	X	X	X	X	1
	Lawn	X	X	X	X	X	1

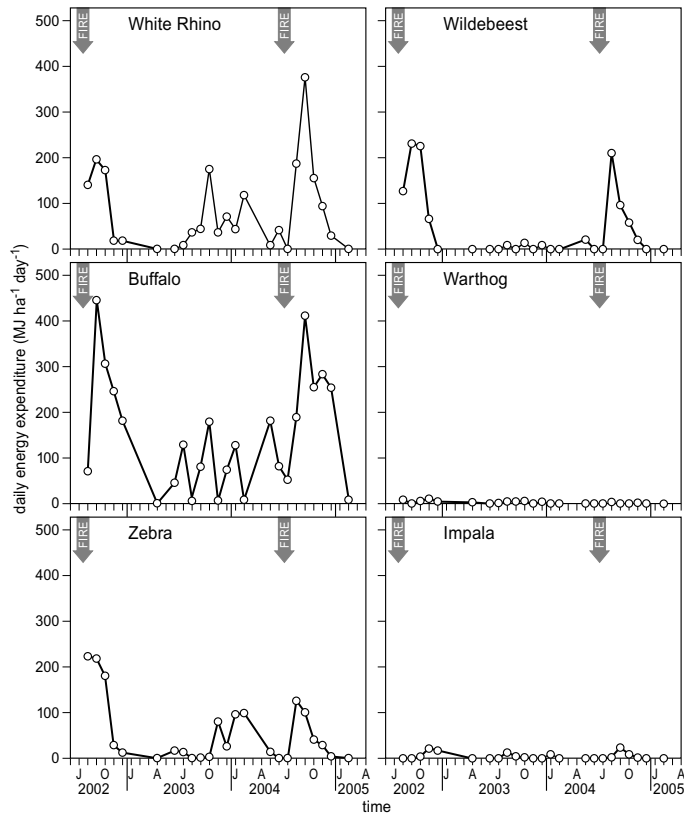


Figure 5 - Monthly averages for daily energy expenditure of 6 grazer species (MJ ha⁻¹ day⁻¹) in the bunch grassland. The arrows show the timing of two fire events (31 July 2002 and 5 August 2004).

Discussion

The grasslands that were dominated by stoloniferous grazing lawn species were characterized by a high overall visitation of a diverse grazer assemblage. We showed that these grassland sites generally offered a better food quality (higher contents of N and several essential minerals), but possibly a lower food availability (grass standing biomass) than the bunch grassland. These lawn-dominated grasslands were situated on relatively sandy soils compared with the clayey soil of the bunch grassland. The three sites also had a different burning regime; the bunch grassland burnt twice during our study period, the mixed site once and the lawn grassland did not burn during this period (Fig. 1). The lawn and mixed site were visited by twice as many species on a daily basis, showing that grassland burning

does not necessarily increase herbivore species richness. The number of grazers visiting per day was highest in the mixed site, ca 1.5 higher than in the lawn site and 4.5 higher than in the bunch grassland (Table 3). Correcting for average species body mass the relative difference between mixed site and bunch grassland was much lower (only 2 times higher), indicating that larger species were relatively more abundant in the bunch grassland. Indeed, buffalo and white rhino dominated the assemblage that visited the bunch grassland, while the smaller grazers (wildebeest, impala and warthog) were more abundant in the lawn dominated sites (Fig. 3). Main difference between mixed and lawn site was a much higher abundance of white rhino and impala in the mixed grassland. DEE remained higher during most of the year on the lawn-dominated grasslands compared with the bunch site, except after a fire event, when DEE in the bunch grassland increased strongly to the level of the other sites (Fig. 4). This post-burn effect lasted 2-3 months and was mainly caused by an increased visitation of Buffalo and Wildebeest (Fig. 5).

Several studies showed that production in grazing lawns is high and possibly higher than in other grassland types (McNaughton 1976, Hik and Jefferies 1990, Ruess et al. 1997). The fact that we expressed food quantity in the grassland as standing biomass might, therefore, strongly underestimate food availability in the lawn and mixed sites. The availability in these sites might actually be higher than in the bunch grassland, especially after periods of sufficient rain. Therefore, on the basis of our data it is difficult to compare grasslands in terms of resource quantity.

The grazing lawn was characterized by a low structural quality in terms of the leaf-stem ratio. The leaf-stem ratio was more than twice as high in the bunch and mixed grassland as in the lawn grassland. However, we showed that nutritional quality in terms of leaf mineral content was generally higher in the grazing lawn and the mixed site (only Ca, Mn and C content were higher in the bunch grassland). Sodium content was 5 times higher in the lawn and mixed sites than in the bunch grassland. The contents of P, N and Cu were 2-3 times higher in the mixed and lawn sites. Moreover, the C/N ratio is twice as high in the bunch grassland as in the lawn and mixed site. Therefore, our study suggests that species select for a higher nutritional quality of the grass in the lawn and mixed site, rather than the structural quality (though the higher leaf-stem ratio of forage in the mixed grasslands might explain the higher grazer abundance in this grassland compared with the grazing lawn). These results confirm McNaughton (1988, 1990) who found that forage in areas that supported high animal densities had higher mineral concentrations than forage in control areas. He, furthermore, suggested that Mg, Na and P are particularly important minerals in shaping herbivore distributions. Our results seem to confirm this suggestion for Na and P. Several other studies have argued that Na and P are the most limiting minerals for wild ranging large mammalian herbivores (Grasman and Hellgren 1993, Hellgren and Pitts 1997, Bruinderink et al. 2000). In our study Mg content did not differ between the highly

visited and less visited sites. Our results rather suggest that selection for Cu instead of Mg may play a role. Copper deficiencies have been reported for a range of wild herbivores world-wide (Robbins, 1993). While McNaughton (1988) discussed concentration of a mix of herbivore species, our results suggest that not all species concentrate on the mineral-rich grasslands to the same extent. It has been proposed that sodium requirement scales to body mass in a similar way as metabolic rate (with a power 0.75), resulting in a lower mass-specific sodium requirement for larger species (Hellgren and Pitts 1997). This might explain why especially the smaller to intermediate-sized grazers (warthog, impala and wildebeest) concentrate on the lawn and mixed site, as shown in our study. In general, however, we have to conclude that, while above-mentioned results indicate the importance of minerals for understanding large herbivore distribution patterns, our knowledge on the role of minerals in determining ungulate distribution and abundance is still very limited. We, especially, need a much better insight in the relative role of the different minerals in spatially and temporally dynamic environments.

The visitation of herbivores to the mixed and lawn site was higher than in the bunch grassland during most of our 2 and half year observation period. Only during the first 2-3 months after a fire the overall visitation of herbivores in the bunch grassland increased to a level comparable with the other grasslands. Visitation to the lawn-dominated sites was, however, certainly not stable over time. Visitation to these sites seemed to be related to rainfall where visitation decreased during the dry season (Fig. 4, seen in 2003 as well as 2004). This response to rainfall, however, was not unambiguous. After all, in 2003 the visitation remained very high for a long period despite strong decline in rainfall. On the other hand visitation in 2004 already declined, while rainfall was still fairly high. Furthermore, the visitation to the mixed site seemed to be more stable with less strong declines in visitation as in the grazing lawn. We need data from more sites and especially over an even longer time period than our study to get a better insight in seasonal use of grazing lawns. The main dynamic in the bunch grassland was the difference in visitation before and 2-3 months after a fire. This magnet-effect of the high-quality grass in post-burn sites has been repeatedly shown (see Tomor and Owen-Smith 2002). The effect has been shown for a large variety of ungulate species and Wilsey (1996) argued that the response of a species to burns depends on its body-mass where small species show a stronger response. In contrast with Wilsey (1996), however, in our study the larger species (buffalo, white rhino and wildebeest) concentrated on the burnt site, while the smaller species (warthog and impala) hardly visited the post-burn site.

Temporal partitioning amongst species in the use of the different grassland types did not seem to play a big role. During our over 2 and a half year observation period we did not observe any strong temporal segregation amongst grazer species in their visitation of the grassland sites. In contrast we found that the visitation of several species was positively correlated in all sites (notably Wildebeest/Zebra

visitation and Impala/Warthog visitation). Temporal partitioning of grass resources has been shown to play an important role in the migratory east African savanna systems (Vesey-Fitzgerald 1960, McNaughton and Georgiadis 1986). These studies were performed in a fairly homogeneous system, where animals migrate between tall and short grass plains, each thousands of hectares in size and lying far apart. In our study system grasslands are much smaller (several hectares) and alternate each other within relatively small areas (few square kilometers). In such a heterogeneous system spatial resource partitioning might be more important. Different species might partition the grass resource spatially within our grassland sites along a grass species, grass height and potentially patch size axis. Studies have shown that all these axes can potentially contribute to resource partitioning amongst grazers in space (Farnsworth et al, 2002; Jarman and Sinclair, 1979; Cromsigt and Olff in press). In this light it is interesting to note that the highest overall daily visitation was found in the mixed site. This site was characterized by a high spatial variation in patches of different grass height compared with the more homogenous bunch and lawn sites. This higher spatial variation might have offered more options for spatial partitioning in the mixed site, resulting in a higher visitation.

We showed that the grasslands that were dominated by stoloniferous lawn grass species, the lawn and mixed site, were characterized by a substantially higher concentration of herbivores throughout the year from a larger variety of species. The bunch grassland was poorly visited, except by buffalo and 2-3 months after a fire. These results indicate that a high variation of grassland types in space contributes to a higher grazer species richness and abundance. This would argue for a management regime that aims at maintaining and/or increasing grassland type heterogeneity. Our results support the studies of Archibald et al (2005) and Fuhlendorf and Engle (2001) who describe exciting new ideas that link management actions to grassland heterogeneity and hypothesize about the effect on herbivore communities. They discuss how the use of fire as a management tool interacts with grazing to influence grassland heterogeneity, especially the relative proportions of lawn and bunch grasslands. Du Toit et al (2003) recently also emphasized the role of managing heterogeneity in savannas. More studies are, however, necessary to come to a predictive science that can give management the necessary input to develop their actions. Though the recent work on the effect of fire management is promising, the interaction with other landscape factors such as altitude, geology, distance to water and former land use is still very unclear (East 1984, Young et al 1995). On this scale one of the main challenges is to come to a predictive science that can support management questions such as what is the minimum proportion of grassland types necessary to sustain high ungulate diversity and how does change in proportion and configuration of these grassland types change this diversity.

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5

Resource partitioning among savanna grazers mediated by local heterogeneity: an experimental approach.

Joris P. G. M. Cromsigt and Han Olff

Ecology, in press

Johan, baba, thanks for your important contribution to our project, while supervising the field team from 2003-2004 and greatly improving the safety situation within the project. It was also good to work with you in your new position as a research technician for Ezemvelo KZN Wildlife in Hluhluwe-iMfolozi Park. I miss the Mr C calls in the office in Hluhluwe...

Abstract

Recent theoretical studies predict that body size-related inter-specific differences in spatial scale of perception and resource use may contribute to coexistence of species that compete for the same class of resources. These studies provide a new theoretical framework for explaining resource partitioning patterns amongst African ungulates that coexist in spatially heterogeneous savanna grasslands. According to these studies different-sized ungulates can coexist because larger species forage at a coarser scale but can tolerate lower quality food, while smaller species need higher quality food but forage at a finer scale. To test this hypothesis in an African savanna, we created an experimental mosaic with variation in grain (spatial detail) and quality of short grass patches and directly observed the visitation of naturally occurring grazers to this mosaic over a 2-year period (total of 903 observation hours). Of the 7 species that visited our experiment warthog, impala, zebra and white rhino visited long enough to allow data analysis. We showed that warthog and impala avoided plots with a finer grain of short grass and that warthog preferred the fertilized above the unfertilized plots. Zebra and White Rhino did not avoid the finer grain plots. Our results suggest that differences in grain and quality of a resource might indeed contribute to partitioning of this resource by savanna ungulates. Although a number of four species is unusually high for an experimental study on resource partitioning amongst naturally occurring savanna ungulates, this number is too low to evaluate the allometric basis of our hypothesis. Our results, however, encourage wider experimental testing of the role of spatial heterogeneity in facilitating the coexistence of potentially competing savanna herbivores.

Introduction

Large African grazers are important both ecologically (Bell 1971, McNaughton 1985, Owen-Smith 1988) and economically (Prins et al. 2000, Gordon et al. 2004) but their diversity and abundance are increasingly threatened by human activities (Prins 1992, Cincotta et al. 2000, Olff et al. 2002). Protected areas often hold a high number of large grazer species that apparently all eat the same grasses while the mechanism of resource partitioning is often unclear (Sinclair 1985). We need more insight in these mechanisms to predict the consequences of increasing ecological isolation of protected areas, and increasing human pressure on unprotected areas. The resource use of African grazers has been intensively studied both theoretically (e.g., Du Toit and Owen-Smith 1989, Illius and Gordon 1992, Gordon and Illius 1996, Arsenault and Owen-Smith 2002) and observationally (e.g., Jarman 1974, Underwood 1983, Voeten and Prins 1999). Using classical niche approaches, these authors conclude that food quality and quantity are the two main niche axes that allow resource partitioning. This is in accordance with the prediction that larger species, having a lower per mass metabolic rate, need large amounts of food but can cope with relatively low food quality, whereas smaller species, with higher per mass metabolic rates, can cope with lower amounts of food but require a relatively high food quality (Coe 1983, Bugalho 1995, Belovsky 1997, Wilmhurst et al. 2000, Olff et al. 2002).

Variation in food quantity has mostly been attributed to variation in the vertical dimension (vegetation height), where different grazers specialize on different heights (Perrin and Brereton 1999, Murray and Illius 2000, Farnsworth et al. 2002). However, variation in food quantity also may arise from variation in horizontal dimensions (patch size). Several studies have shown the impact of vegetation patchiness on herbivore foraging behavior (Wilmhurst et al. 1995, Hester et al. 1999, WallisDeVries et al. 1999, Fryxell et al. 2004) but there are few studies examining the effect of such patchiness on local resource partitioning in diverse herbivore assemblages. Resource partitioning along the quality axis has mostly been studied theoretically (Illius and Gordon 1992, Gordon and Illius 1996, Belovsky 1997) with few experimental tests in the field. The above-mentioned studies on food quantity as well as quality suggest that savanna herbivores can coexist if spatial heterogeneity in food quality and food quantity is implicitly assumed. However, the difficulty in making this spatial component explicit in analytically tractable models so far has restricted the application and experimental test of these insights to further understand grazer coexistence in savannas.

Using principles of fractal geometry, Ritchie and Olff (1999) incorporated spatial heterogeneity and scale into niche dimensions of local food abundance and food quality to explain the coexistence of different-sized species (see also Olff and Ritchie 2001, Haskell et al. 2002, and Ritchie and Olff 2004). They suggested that larger species should perceive and use less spatial detail (coarser grain) of heterogeneously distributed resources. They show theoretically how these

differences in scale of resource perception combined with variation in patch size and resource quality within patches can explain the coexistence of different-sized species. Within a size hierarchy, species may use resources exclusively in patches that are of too low resource concentration for the next smaller species and meanwhile are too small for the next bigger species. The size-ratio (the relative difference between two species that are next to each other in the size hierarchy), and hence the number of species, will be set by variation in resource availability and the size of these 'exclusive spatial niches,' so that populations of all species can be sustained. Based on only the presence of the exclusive spatial niches, this model predicts a minimum number of species that can be sustained without having to understand the outcome of resource competition in the patches that are used jointly by different species. This new explanation for resource partitioning in spatially structured habitats has not yet been tested experimentally.

We designed an experiment in which we manipulated the scale of resolution (grain) and resource quality of patches of short grass and followed the visitation of different grazer species. The experiment was performed in a South African savanna with a complete and diverse large-grazer assemblage. We specifically tested whether scale of resolution and quality can form axes along which large grazers partition resources. Additionally, we tested whether resource partitioning along these axes had an allometric basis as expected by Ritchie and Olff (1999).

Methods

Study area

The study was performed in the Hluhluwe-iMfolozi Park, an 89,665 ha reserve in Kwazulu-Natal, South Africa. Mean annual rainfall varies from 985 mm in high altitude regions to 650 mm in lower areas and mainly falls between October and March. Daily maximum temperatures range from 13 to 35 °C. The park is inhabited by a complete set of indigenous large herbivores and carnivores (Brooks and MacDonald 1983), including 7 species that have grass as a major component of their diet: white rhino (*Ceratotherium simum*), African buffalo (*Syncerus caffer*), plains zebra (*Equus burchelli*), blue wildebeest (*Connochaetes taurinus*), waterbuck (*Kobus ellipsiprymnus*), warthog (*Phacochoerus aethiopicus*), and impala (*Aepyceros melampus*).

Experimental design

The experiment was set up in the northern part of the reserve, with a yearly average rainfall of approximately 700-800 mm. Manipulations were performed in an open savanna, dominated by the tall grasses *Eragrostis curvula* and *Panicum maximum* with bush encroachment of *Dichrostachys cinerea*, *Acacia* spp. and *Gymnosporia senegalensis*. May 2000 we created an experimental mosaic of different-sized short grass patches in the tall, woody matrix vegetation using a brush cutter and we subsequently maintained the mosaic with a lawn mower at a

height of approximately 5 cm. After about one year the grazing pressure kept the grass at approximately this height and, at that point, we stopped mowing.

We manipulated resource quality and scale of resolution in a basic layout of adjacent 8×8-m treatment plots (Fig. 1). In this set-up the mown short-grass patches represent the resource offered in 8×8-m treatment plots. We created differences in scale of resource resolution by varying the size and number of short grass patches in the 8×8-m plots. As shown in Fig. 1, the amount of short grass and the configuration of short grass patches in an 8×8-m treatment plot are confounded factors. We, therefore, use the term grain aiming at both two factors. If we talk about a plot with coarser grain, this plot has a larger amount of short grass and at the same time the short grass in the plots is less fragmented. Our design included 4 levels of resource grain, varying from fine to coarse grain; i.e. 9 1×1-m (G1), 4 2×2-m (G2), 2 4×4-m (G4), and 1 8×8-m (G8) short grass patches per 8×8-m plot (Fig. 1) Note that the total area short grass increases proportionally between grain levels. The variation in grain of short grass, which we created, corresponded with the range of natural grazing lawn patches that occurred in the area surrounding the experiment at a low density.

To create resource quality differences we applied an artificial slow-release fertilizer to the mown short grass in half of the 8×8-m plots every 3 months for 2 and half years; from June 2000 up to November 2002. With this approach we expected to create a more or less constant nutrient supply. To patches of all grain sizes we applied 12 g N, 3.9 g P, 19.8 g K, 22.1 g Ca and 18.8 g S per m² short grass per year. The nutrient treatments were coded with U (unfertilized) or F (fertilized).

The experimental design resulted in 8 treatment combinations, with, e.g., G4U being the 4×4-m grain, unfertilized patches. Each combination of grain and

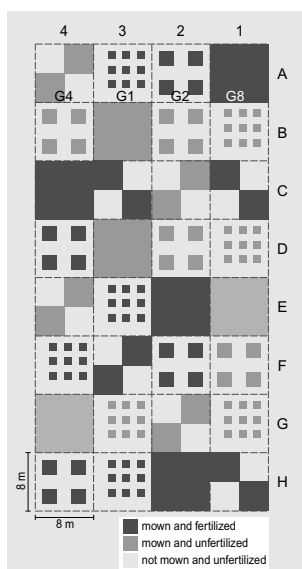


Figure 1 - The experimental layout, existing of 8 x 8 meter treatment plots with a combination of two treatments (patch size and fertilizer application). Manipulated patches are shown in black and grey; the shaded background represents the untreated matrix of tall grass and shrubs. Half of the plots were fertilized (black) and the other half remained unfertilized (grey). Within each 8x 8 m plot, we created 4 different levels of spatial scale of short grass patches: 9 patches of 1 x 1m (G1), 4 patches of 2 x 2 m (G2), 2 patches of 4 x 4 meter patches (G4) and 1 patch of 8 x 8 meter (G8).

fertilization was replicated 4 times. This resulted in 32 8×8-m plots that were situated next to each other (Fig. 1) to be able to easily oversee the whole experiment.

Effects of the treatments on the vegetation

In July 2002 we took grass samples to determine leaf nitrogen concentrations. We clipped all aboveground grass material within 5 randomly placed 50×50 cm frames in the short grass subplots of each treatment plot. Before clipping the total aerial vegetation cover (%) was estimated for each frame. Clipped material was dried for 48 hours at 70 °C. For each sample we measured the total dry weight (DW), the DW of the leaves as a % of total DW, the DW of the stems (%) and the DW of the dead organic matter (% DOM). Subsequently we pooled the 5 dried leaf samples per 8×8-m plot and ground and analyzed each pooled sample for total nitrogen content (as a % of leaf dry weight) according to the Macro-Kjeldahl method (Donkin et al. 1993). In September 2002 we recorded grass species composition in 5 randomly placed 50×50 cm frames in the short grass subplots of each treatment plot. Within each frame the 5 dominant grass species were identified. The species were ranked according to their total cover in the frame, receiving a dominance rank from 1 to 5 (in order of increasing cover).

Animal visitation

The experimental site was situated on a hill slope and, using binoculars, we observed grazer visitation from a car that was standing hidden between trees at the opposite hillside (about 450 m from the experiment) to avoid disturbing the animals. Between October 2000 and November 2002 we observed the experiment 4 times a week in periods of 3 hours (divided over early morning and late afternoon sessions), except in case of bad weather, which made observations impossible. In total we carried out 329 observation periods, resulting in a total of 903 observation hours. During an observation period, we scanned the experimental site for the presence of animals after every 5 minutes. When an animal was present, every minute the position of the animal in the mosaic was recorded according to the grid that is shown in Fig. 1, i.e. per 8×8-m plot. Next to the position we recorded the animal's behavior (grazing versus non-grazing, e.g., grooming or looking around) and whether individuals were grazing in mown short grass patches versus tall matrix vegetation.

Data analysis

Effect of treatments on the vegetation

Before further analysis, we averaged the dry weight (DW), % vegetation cover and species dominance rank values of the 5 samples that we took per 8×8-m treatment plot. We already had 1 value per treatment plot for %N, because samples were pooled before N analysis. We tested the effects of the treatments on these variables with two-way analyses of variance followed by Student-Newman-Keuls *a posteriori* contrasts.

Effect of fertilizer application on animal visitation

We expressed animal visitation as the total time an individual of a particular species was observed grazing in the short grass subplots of each 8×8-m plot as a percentage of the total observation time (903 h). Besides grazing in the short grass plots, the total observation time existed of time when no animal was observed and when animals exhibited non-grazing behavior or grazed in the matrix vegetation. We did not identify individuals; i.e. 20 minutes of grazing within the experimental area could consist of the same individual grazing 20 minutes, or two individuals grazing together for 10 minutes.

We first tested for an effect of fertilizer application and grain on animal visitation with an analysis of variance, followed by Student-Newmann-Keuls contrasts. As mentioned, 8×8-m plots with a coarser grain also have a larger total area short grass. Randomly distributed grazing animals (without preference for a particular grain) would be expected to graze longer in plots with a coarser grain. Therefore, this statistical design permits us to study the effect of fertilizer application, and possible interactions with grain level, rather than testing a preference for finer or coarser grain.

Animal preference for plots with finer or coarser grain

To analyze whether animals preferred a finer or coarser resource grain, corrected for the total area short grass available in each grain level, we performed a scaling analysis. This scaling analysis is based on the proportional increase of total area short grass between grain levels. We introduce a scaling exponent γ that represents the preference of a certain species for a finer or coarser grain by exploring whether the percentage of total time observed grazing in an 8×8-m plot (Q) scaled with total area short grass (A) in that 8×8-m plot as $Q = c \times A^\gamma$. If γ is equal to 1 then Q increases proportionally with A , meaning that the species does not clearly prefer a finer or coarser grain (e.g., a two-fold increase in area short grass in an 8×8-m plot leads to a two-fold increase in grazing time). If γ is different from 1 the species displays a disproportionate preference for coarser ($\gamma > 1$), or finer ($\gamma < 1$) grain of short grass patches, where the value of γ represents the magnitude of preference or avoidance.

We first calculated Q as the average % grazing time for each treatment combination ($n = 4$). We estimated γ for each of the grazer species, based on these 8 average grazing time values, as the slope of the linear regression of $\log(Q)$ over $\log(A)$. In addition to the fit of the regression (R^2 and level of significance), we also estimated the 97.5 confidence intervals for γ to indicate whether γ is likely to differ from 1 ($\alpha = 0.05$).

Influence of context of treatment plots on plot selection

In the previous analysis we analyzed animal preference for resource grain on the 8×8-m plot level. The advantage of this analysis was that the grazing time for each grain level was the result of an average of 4 replicates. This analysis, however, did not account for the different context that surrounded each replicate (see Fig. 1, e.g. plot A1 (treatment G8F) was surrounded by matrix, two G2 plots and 1 G1 plot,

while plot E2 (also G8F) is surrounded by 2 G8, 1 G4, 3 G2 and 2 G1 plots and no matrix). We performed another analysis to test whether the context of a treatment plot influenced the selection of that plot. We divided the experiment in a 1×1-m grid and for each grid cell we calculated the proportion of nearby cells with short grass (p_l) for different window lengths l around that cell (3, 5, 7, 9, 11, 13, 15, 17 and 19 m). We used this range of window lengths to vary the context of each treatment plot because beforehand we did not know the size of the context that would influence the selection of an animal of a certain plot. To calculate an average short grass context for each 8×8-m treatment plot, we averaged the 64 values of p_l for each 8×8-m plot and each window length. Per window length, we sorted the 32 8×8-m plots by increasing average p_l value and then aggregated the 32 values into 8 classes calculating an average % grazing time and average p_l per class. Based on these 8 averages, we estimated γ as the B coefficient from a linear regression of $\log(Q)$ over $\log(p_l)$ and provided 97.5 confidence intervals for γ to indicate whether γ significantly deviated from 1 ($\alpha = 0.05$). We performed these regressions for all 4 species for all 9 window sizes l .

Table 1 - The effect of fertilizer application and grain of short grass patches on properties of the above-ground grass biomass. DW = total aboveground dry weight (g per 0.25 m²); % Leaf, Stem, DOM = % dry weight leaves, stems or dead organic matter of total dry weight; L/S = leaf - stem ratio (% Leaf / % Stem); Leaf N = N content of the leaves as a % of leaf dry weight; Cover = % of 0.25 m sq that is covered by vegetation (aerial cover). The results are based on samples that were clipped in July 2002. The table shows the means (n=4), different superscript letters indicate a significant difference within a variable between treatments ($P < 0.05$, Student-Newman-Keuls test after two-way analysis of variance). There were no significant interactions between treatments.

Grain	Fertilization	DW (g)	% Leaf	% Stem	% DOM	L/S	Leaf N (%)	Cover (%)
G1	Fertilized	3.32 ^a	39 ^a	12 ^a	49 ^a	4.43 ^a	2.33 ^a	15.50 ^a
G2	Fertilized	4.13 ^{ac}	49 ^a	14 ^a	37 ^a	4.65 ^a	2.78 ^a	27.00 ^b
G4	Fertilized	4.19 ^c	41 ^a	16 ^a	43 ^a	3.25 ^a	2.42 ^a	38.50 ^c
G8	Fertilized	5.04 ^c	43 ^a	18 ^a	39 ^a	2.92 ^a	2.84 ^a	43.50 ^c
G1	Unfertilized	4.50 ^b	30 ^b	11 ^a	58 ^b	3.58 ^a	2.00 ^b	16.50 ^a
G2	Unfertilized	8.58 ^{bd}	32 ^b	15 ^a	53 ^b	2.45 ^a	2.29 ^b	27.50 ^b
G4	Unfertilized	10.43 ^d	26 ^b	12 ^a	61 ^b	2.96 ^a	2.06 ^b	46.50 ^c
G8	Unfertilized	10.43 ^d	29 ^b	10 ^a	61 ^b	3.63 ^a	2.01 ^b	51.75 ^c

Results

Effect of treatments on the vegetation

The 5 most abundant grass species in the short grass subplots towards the end of the experiment were (with their average dominance rank): *Eragrostis curvula* (4.0), *Eragrostis superba* (3.7), *Urochloa mosambicensis* (1.3), *Panicum maximum* (1.1) and *Digitaria longiflora* (1.0). Four other additional grass species were found with lower abundances: *Themeda triandra*, *Bothriochloa insculpta*, *Heteropogon contortus* and *Sporobolus pyramidalis*. The vegetation composition

in terms of dominant grass species did not differ among treatments ($P > 0.05$). As mentioned in Methods the surrounding matrix was dominated by the grasses *Eragrostis curvula* and *Panicum maximum*.

The percentage total cover of the vegetation was significantly higher in the G8 and G4 plots than in the G2 plots and higher in G2 than in G1 ($F_{3, 24} = 21.5$, $P < 0.01$, Table 1). The total aboveground dry weight in the G1 treatment was lower than in G4 and G8, while G2 had an intermediate weight ($F_{3, 24} = 3.3$, $P < 0.05$, Table 1). Fertilizer application reduced the aboveground total dry weight ($F_{1, 24} = 20.8$, $P < 0.01$) and the % dead organic matter ($F_{1, 24} = 36.3$, $P < 0.01$, Table 1), probably due to higher grazing pressure. The percentage leaves of total biomass ($F_{1, 24} = 40.1$, $P < 0.01$) and the nitrogen concentration of the leaves ($F_{1, 24} = 5.7$, $P < 0.05$) was higher in the fertilized plots than in the unfertilized plots (Table 1). The percentage stems of total biomass and the leaf/stem ratio did not differ between grain size and fertilizer application treatments (Table 1).

Animal visitation

During our observations, the experiment was visited by all grazer species present in the reserve. Buffalo, waterbuck and wildebeest, however, were observed grazing for only a low number of minutes (less than 20 minutes). Impala, warthog, white rhino and zebra were observed grazing long enough to allow statistical analysis: 1798, 2737, 105 and 674 minutes (no. of individuals \times time observed) respectively.

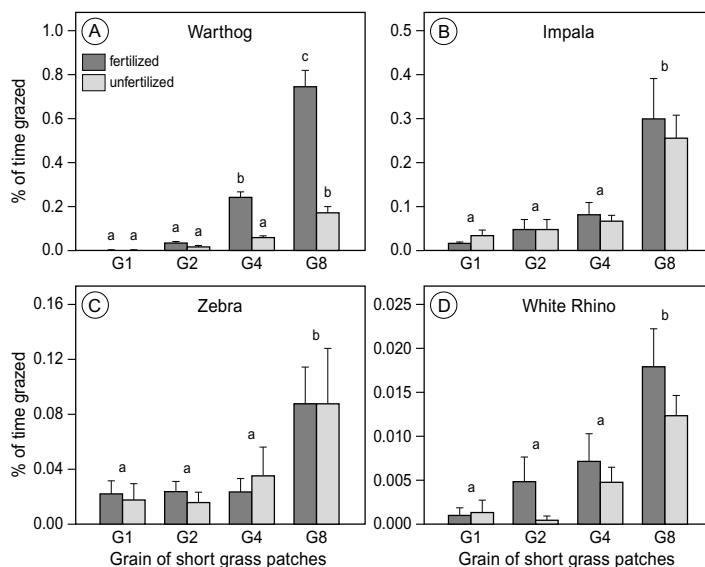


Figure 2 - Mean percentage (± 1 s.d.) of the time grazed by four grazer species of the total observation time in the 8 \times 8 meter plots, for different levels of grain of short grass patches (see Fig. 1) and fertilizer application treatment. Different letters indicate a significant difference between treatments ($P < 0.05$, Student-Newman-Keuls test after two-way analysis of variance).

Effect of fertilizer application on animal visitation

Impala, zebra and white rhino visited the fertilized plots as long as the unfertilized plots ($F_{1,24} = 0.173$, $P = 0.681$; $F_{1,24} < 0.001$, $P = 0.987$; $F_{1,24} = 2.737$, $P = 0.111$, respectively). All three species visited the plots with the coarsest grain (G8) more than the other grain levels ($F_{3,24} = 16.892$, $P < 0.001$; $F_{3,24} = 5.329$, $P = 0.006$; $F_{3,24} = 12.326$, $P < 0.001$, respectively). Fertilizer application positively influenced warthog visitation, but this effect depended on grain level (interaction fertilization \times grain, $F_{3,24} = 35.622$, $P < 0.001$). Warthog visited the fertilized plots more than the unfertilized plots but only for the plots with coarser grain, G4 and G8 (Fig. 2A). Data in Fig. 2 show the visitation of the 8x8 treatment plots uncorrected for the differences between the treatments in the total area of short grass (which was however the same for the fertilizer application treatments).

Animal preference for plots with finer or coarser grain

Fig. 3 shows the preference of species for a finer or coarser grain, corrected for the total area of short grass per grain level. Warthog disproportionately avoided

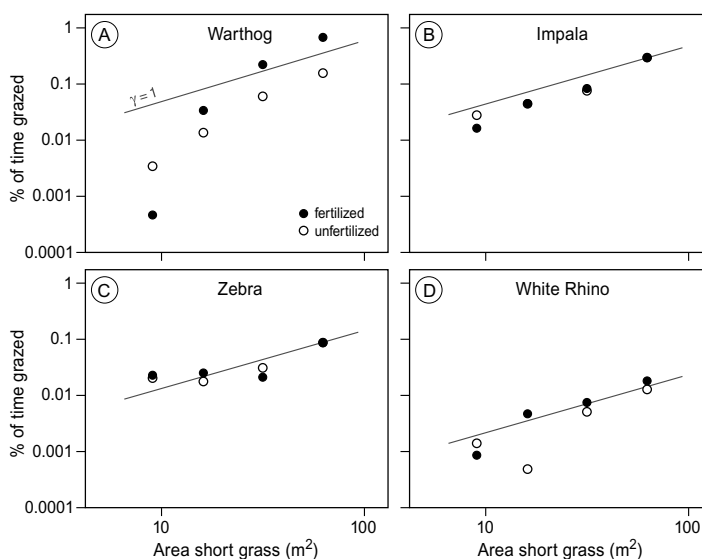


Figure 3 - Scaling of the percentage of time grazed with the total area of short grass per treatment plot on a log-log axis. The symbols represent average % of time grazed ($n = 4$) for eight treatment combinations; 4 levels of total area short grass per 8x8-m plot (9, 16, 32 and 64 m^2) times 2 fertilization levels (solid dots show the fertilized plots and open dots represent the unfertilized plots). The slope, γ , of the regression through the 8 points captures the preference or avoidance of each species for the grain (spatial detail) of area of short grass. When γ is different from 1 the species has a disproportionate preference for a coarser ($\gamma > 1$), or finer ($\gamma < 1$) grain. The line represents the situation of no disproportionate preference with a γ of 1. The results of the regressions for the different species are as follows (within brackets is the 97.5% confidence interval of γ), warthog: $\gamma = 2.8$ (1.3-4.3), $R^2 = 0.84$, $P = 0.001$; impala: $\gamma = 1.2$ (0.78-1.69), $R^2 = 0.91$, $P = 0.000$; zebra: $\gamma = 0.7$ (0.18-1.26), $R^2 = 0.72$, $P = 0.008$; white rhino: $\gamma = 1.4$ (0.34-2.43), $R^2 = 0.72$, $P = 0.008$.

finer grain mosaics ($\gamma = 2.8$ with lower confidence interval > 1). The slope of $\gamma > 1$ implies that the warthog's visitation of smaller patches declined faster than expected from the decline in area of short grass in these 8x8-m plots (Fig. 3). This decline is faster in the fertilized plots than in the unfertilized plots (analysis of covariance with area short grass as a covariate, interaction fertilization \times area short grass; $F_{1, 28} = 104.375$, $P < 0.001$). The decline in visitation by impala, zebra and white rhino towards finer grain was not significantly different as expected from the decline in the area of short grass towards these treatments (γ not different from 1, Fig. 3).

Influence of context of treatment plots on plot selection

The R^2 of the regression of log % of time grazed (Q) of the 4 species over log proportion of short grass in neighboring cells (p_l) in a window around a 1x1-m cell declined for warthog, impala and white rhino with increasing window length l (Fig. 4).

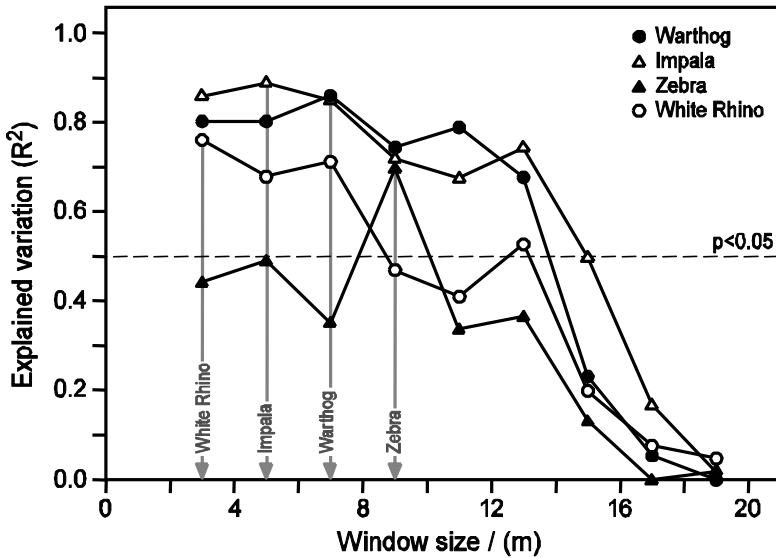


Figure 4 - Explained variation (R^2) of regressions of % of time grazed versus the proportion of grass in nearby cells around each 1x1-m cell, for a range of window sizes (3-19 m), reflecting different scales of resource perception. Results are shown for warthog (solid dots), impala (open triangles), zebra (solid triangles), and white rhino (open dots). The arrows show the scale of perception (window size) for the 4 species that had the best fitting regression. The results of these best fits are as follows (within brackets is the 97.5% confidence interval of γ), warthog: $\gamma = 3.5$ (1.8-5.1), $R^2 = 0.86$, $P = 0.0008$; impala: $\gamma = 2.1$ (1.2-2.9), $R^2 = 0.89$, $P = 0.0004$; zebra: $\gamma = 1.2$ (0.3-2.2), $R^2 = 0.70$, $P = 0.0094$; white rhino: $\gamma = 1.8$ (0.6-3.1), $R^2 = 0.76$, $P = 0.0048$.

The proportion of short grass in window of lengths > 14 m did not explain further spatial variation in visitation of these three species, as the fit of the regressions steeply declined beyond this scale and were not significant. With window size smaller than 14 m, the fit for warthog and impala did not change much, while the fit for white rhino kept improving. For zebra, only the proportion of short grass within window lengths of 9 m contributed significantly to explaining the spatial variation in visitation, and regressions at the other scales were not significant (Fig. 4). Thus the approximate spatial scale at which the % of time grazed correlated best with proportion of grass in neighboring cells declined from zebra, to warthog and impala, to white rhino. The analysis in Fig. 4 also showed that for the regression with the best fit (with $l = 5$) impala disproportionately avoided finer grain mosaics ($\gamma = 2.1$ with lower confidence interval > 1).

Discussion

Our results showed that differences in resource concentration and grain of experimentally manipulated short grass patches might create opportunities for spatial resource partitioning between different grazer species. In contrast to the other species, warthog preferred the plots with a coarser grain of short grass, especially if these plots were fertilized (Fig. 2 and 3). Fertilization of the plots increased N content of the leaves and proportion of leaves of above-ground dry weight and reduced the proportion of grass dead standing biomass. When we included the context of treatment plots in our analysis impala visitation per m² of short grass, like that of warthog, decreased towards finer grain mosaics (Fig. 4). Zebra and white rhino maintained a constant visitation per unit area of short grass, despite a finer resource grain with and without including the context of treatment plots in our analysis (Fig. 2 and 4). Our results also suggested that the extent of the context that influenced plot selection differed between species. This extent declined from zebra, warthog and impala to white rhino (Fig. 4). This suggests that the largest herbivore species had the finest scale of resource selection.

With our experimental study in a natural environment we chose a site-centered approach to studying resource partitioning among naturally occurring grazers. This time-demanding approach has been rarely used and has the advantage of directly observing individuals of species that come from the same local grazer assemblage pool and that can select from the same available resource patches during the same time period. Most studies on resource partitioning amongst African ungulates have been animal-centered studying animal food preferences only on those random locations where a certain herbivore is seen (e.g., Underwood 1983, Voeten and Prins 1999) and, therefore, often have the problem that species comparisons have to be based on data that originate from different sites and sometimes different time periods, potentially leading to spurious correlations. The few studies that did choose a site-based experimental approach generally had a focus on individual foraging behavior instead of community ecology, therefore including only 1 or 2 species (e.g., Wilmschurst et al. 1995, Wallis

de Vries et al. 1999), making it difficult to use their results to discuss general resource partitioning mechanisms.

As mentioned in Methods the amount and the configuration of short grass patches are confounded factors in our experimental design. One could argue that these factors should be tested separately in a factorial design. However, a design where we would keep the amount constant and vary the configuration has other major disadvantages. In such a design the spatial extent of the treatment plots would not be the same (e.g. we would get an 8×8-m treatment plot for the coarsest grain of 1 64 m² short grass patch and a 17×17-m treatment plot for the finest grain with 64 1 m² short grass patches). First of all, using this design the whole experimental area would become too large to oversee at one glance, making it practically impossible to directly observe animals. Secondly, a significant increase of the total experimental area would have implications for the amount of underlying heterogeneity that is covered by the study; e.g. the natural underlying variation in soil fertility. Different-sized treatment plots would vary in the cover of this underlying heterogeneity, where it would be larger in the larger treatment plots than in the smaller plots. Therefore, we chose for a design where we kept treatment plot size constant and proportionally increased the total area short grass between grain levels so that we could use a scaling analysis to test preference for grain level.

Our results did not confirm the central hypothesis of Ritchie and Olff (1999) that larger herbivore species sample resources at a coarser resolution than smaller species. After all, in our study the smaller species, warthog and impala, selected for coarser grain plots. However, there are several reasons why we can also not refute their hypothesis, such as the limited number of species in our analysis, the scale of our experiment and confounding factors such as the influence of group size and predator avoidance behavior.

The fact that we could only analyze a limited number of four species makes it difficult to test the allometric nature of the hypothesis of Ritchie and Olff (1999). This is a generally recognized problem with experimental tests of macro-ecological theories, where autecological differences overrule the general macro-ecological patterns in a limited set of species. We, however, want to emphasize that the number of four species in itself is not a low number for an experimental test of resource partitioning amongst savanna ungulates. As discussed earlier there are hardly any site-centered studies that experimentally test resource partitioning patterns that include more than one or two species.

Ritchie and Olff (1999) did not explicitly state the relevant range of scales over which they might expect the allometric scaling to occur for different groups of species. Whether the theory holds across other scales is still open for debate and empirical testing. We chose to test their model at the scale of resource patches varying in size from 1 to 64 square meters. The allometric relation might, however, become apparent at larger scales, where larger species are more abundant in landscapes that are dominated by large (several hectares) high quality resource patches (such as post-burn grasslands or fertile floodplains), while smaller species

are more prevalent in landscapes that are characterized by a high proportion of small high quality resource patches (e.g. related to trees that locally enhance nutrient availability, Ludwig et al. 2004). On the other hand, the allometric scaling hypothesis might also work on scales smaller than our experiment within a food patch, where smaller grazers select for high quality parts within a plant and larger grazers forage on the whole or a bunch of plants (hereby increasing quantity but decreasing quality of a bite). The original hypothesis, therefore, has to be more widely explored on other scales and locations before we can reject it. The challenge will be to develop appropriate observational and experimental studies on these other scales.

Next to the mentioned issues of scale and number of species there are some confounding factors that hamper the analysis of our results in the light of the allometric hypothesis, i.e. the role of group size and predator avoidance. Hester et al. (1999) suggested that the use of resource patchiness by herbivores relates to their social group size, where an increased group size limits utilization of smaller patches. In their study, solitary sheep chose smaller patches than red deer that foraged in small groups. In our study 100% of the rhino observations existed of individual animals in contrast with around 60% for the other 3 species. The average group size of the 4 species in Hluhluwe-iMfolozi GR exists of 2.3 individuals for warthog, 2.0 for white rhino, 4.1 for zebra and, 8.1 for impala (unpublished data, Ezemvelo KZN Wildlife). Multiplying these average group sizes with an estimate for individual daily energy expenditure (DEE) as two times basal metabolic rate: $DEE = 2 \times 70 \times (\text{body mass})^{0.75} \times 0.004184 \text{ MJ day}^{-1}$ (Demment and Van Soest 1985) we come to a ranking in increasing order of the estimated DEE of an average group of each species (MJ day^{-1}); warthog (36), impala (96), zebra (148) and white rhino (390). Based on this ranking we would expect warthog to select finer grain resources compared with the other species, however in our study warthog selected coarser grain. However, reflecting back on issues of scale, our largest plots might already be too small for the species with the higher DEE of an average group size. This might also explain why buffalo hardly visited the experiment (with a high estimated value of 596 MJ day^{-1}). In conclusion group size differences between species might be very important and should be taken into account in future tests of the allometric hypothesis.

Another factor that might confound the testing of the Ritchie and Olff (1999) hypothesis is that not only the partitioning of food resources but also predation can shape African ungulate communities (Sinclair 1985). Sinclair et al. (2003) showed that smaller herbivore species in the Serengeti encounter greater predation risk than larger herbivores. Moreover, Sinclair et al. (2003) suggested a threshold body weight of 150 kg marking a transition from predator-limited to resource-limited population dynamics. Following this argument, warthog and impala would be more limited by predation than food availability. Other studies have suggested that a higher predation risk stimulates animals to choose more open areas (Underwood 1982). This would suggest that our coarser experimental

plots could be perceived as safer (better view) and may explain the preference of warthog and impala (Fig. 3 and 4) for the coarser resource mosaics. Moreover, note that the species that avoids finer grain most strongly, warthog, is also the smallest of the 4 species. In contrast with the other 3 species it was more difficult for warthog to look over the tall vegetation surrounding the short grass patches. Thus, warthog might have selected for the coarser grain plots as a predator avoidance strategy.

As discussed there are still some significant hurdles that we have to take while experimentally testing the suggested allometric basis of resource partitioning in spatially heterogeneous savannas. But we think that our study is an important first step in dealing with some of these problems. Moreover, we present some of the first experimentally based results that suggest that differences in grain of short grass patches might create opportunities to partition resources amongst savanna ungulates. We showed that warthog and impala preferred coarser grain of short grass patches, while Zebra and White Rhino had no preference for the level of grain. These results seem to justify the increasing focus on the role of spatial heterogeneity in savanna systems (Du Toit et al 2003) which is needed to advance the further understanding of the coexistence and diversity patterns of African ungulate species.

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