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Resource partitioning along multiple niche dimensions in differently sized African savanna grazers

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Resource partitioning among mammalian savanna herbivores is thought to be predominantly driven by differences in body size. In general, large herbivore species utilize abundant low quality forage while small herbivores focus on scarcer high quality food items. However, in a natural system other factors such as digestive strategy, season and the presence of megaherbivores (body size > 1000 kg) are likely to complicate allometric predictions. Non-ruminants are probably better able to cope with abundant low quality food than ruminants of the same size causing a non-ruminant to act 'larger' than allometrically predicted. Also, the effect of alternating seasons with high and low food availability on diet choice and hence the competitive interactions between co-occurring herbivores is still poorly understood. Lastly, how megaherbivores deviate from allometric predictions (based on smaller species) is still not well quantified.

In this study we examine resource partitioning among three ruminant and three non-ruminant grazers: impala, wildebeest, buffalo, warthog, zebra and white rhinoceros (megaherbivore) in the savanna of Hluhluwe iMfolozi Park, South Africa. We analysed habitat and diet overlap, specifically grass species (something not commonly investigated) and grass height eaten, in both the wet and the dry seasons. We found that habitat utilization differences among the species were generally small and did not vary between seasons. Diets within feeding patches overlapped during the wet season but highly diverged during the dry season. Body mass differences among species explained their dry season resource partitioning for all species except for comparisons with the megaherbivore (white rhino), while differences in digestive strategy were not related to niche overlap in either season. We conclude that savanna herbivores in this system coexist mostly through body size-driven resource partitioning in the dry-season, with the exception of the white rhino (megaherbivore).

The African savannas harbor a remarkably high diversity of mammalian herbivores which all rely to a large degree on the same food resource (grass). This paradox of high species diversity and their common reliance on a single resource has fascinated ecologists for decades (Vesey-Fitzgerald 1960, Bell 1971, Cromsigt and Olff 2006). Among savanna herbivores the main driver of resource partitioning is thought to be differences in body size (Illius and Gordon 1993, Gordon and Illius 1996, Prins and Olff 1996, Belovsky 1997, Ritchie and Olff 1999). Multiple species have been suggested to coexist because herbivores of different size utilize forage of different quality and abundance (Vesey-Fitzgerald 1960, Bell 1970, 1971, Jarman 1974, McNaughton 1976, Jarman and Sinclair 1979, Illius and Gordon 1987, 1992, 1993).

Allometric relations between body size and metabolic rate and body size and gut capacity suggest that larger herbivores can survive on lower quality but require higher bulk intake diets while smaller species require higher quality, but sustain on lower bulk intake diets (Bell 1970, Jarman 1974, Demment and Van Soest 1985). These allometric arguments predict that the more similar species are in size the more they

should overlap in niche use. This prediction has, however, been rarely tested using habitat and diet assessments of multiple species within the same ecosystem.

Although allometric relations provide clear predictions as to how herbivore assemblages should be structured, several other factors such as digestive strategy, potential deviations from allometric predictions by herbivores with very large body sizes (megaherbivores) and variations in quality and quantity of forage between seasons may act to dilute the impacts of body size on resource partitioning. Digestive strategy has been suggested to have an important impact on the quality of food that a herbivore can eat and thus may obscure allometry in structuring herbivore communities (Demment and Van Soest 1985, Illius and Gordon 1992, Cromsigt et al. 2009). Non-ruminants are generally less efficient at extracting nutrients from forage than ruminants, especially at intermediate qualities, but compensate for this by having higher throughput rates (Duncan et al. 1990). These increased throughput rates enable non-ruminants to be more effective at processing very low quality forage than a similar size ruminant (Demment and Van Soest 1985, Owen-Smith 1988,

Duncan et al. 1990). Consequently, a non-ruminant of a certain size is expected to overlap in diet more with bigger ruminants than with ruminants of the same size (Illius and Gordon 1992, Murray and Illius 1996).

Megaherbivores (defined as herbivores weighing more than 1000 kg), are considered to play a special role in savannas, i.e. as key stone species (Owen-Smith 1988, Waldram et al. 2008). Also, because they are present in relatively high abundances in many natural ecosystems in Africa, they are an important but commonly overlooked actor in resource partitioning studies (but see Eltringham 1974, de Boer and Prins 1990, Arsenault and Owen-Smith 2008, Crooms et al. 2009). With regards to dietary preferences, allometric relations would predict that megaherbivores should be bulk feeders capable of utilizing the very lowest quality forage when compared to smaller species. However, Owen-Smith (1988) shows that even during the dry season megaherbivores exhibit protein levels (in their stomach contents) comparable to those of much smaller grazers, such as impala *Aepyceros melampus* and wildebeest *Connochaetes taurinus*. The reason for this allometric deviation in diet quality may be related to digestive strategy and to constraints on intake rates and throughput rates of food (Demment and Van Soest 1985, Owen-Smith 1988, Clauss et al. 2007a, 2007b), which particularly act in megaherbivores. Digestion efficiency of plant material is related to mean retention time (MRT) of food in the gastrointestinal tract. Factors determining MRT of food are still largely debated and arguments either revolve around the allometric relationship between body mass and MRT (body mass is positively related to gut volume and hence ingesta retention) (Demment and Van Soest 1985, Owen-Smith 1988) or around quantity of organic matter eaten and MRT (organic matter intake and MRT of the food tend to be negatively related) (Clauss et al. 2007a). In addition to the above arguments Clauss et al. (2007b) has demonstrated, using megaherbivores, that MRT of food may also partly be a species specific trait and that this can be used to predict the feeding ecology and activity budgets of herbivores. For example, in hippopotamus *Hippopotamus amphibius* the retention time of food is strongly related to quantity eaten and thus hippo optimize energy gain on a low bulk, high quality diet and are observed to feed for only 30% of the day. In contrast, elephants *Loxodonta africana* are hardly constrained by the relationship between quantity eaten and MRT and are observed to feed for long periods of time (75% of day) and to eat high bulk low quality diets (Clauss et al. 2007b). White rhinos *Ceratotherium simum* are intermediate in the length of time they spend feeding (50% of day) (Owen-Smith 1988) and if the arguments of Clauss et al. (2007b) are correct this would explain why white rhino are often observed to feed on a higher quality diet than predicted by their body size. It seems (particularly in megaherbivores) that other factors in addition to body size may impact MRT and it is, therefore, important to include these species to fully understand the dynamics of resource partitioning.

A further complication of using body size alone to predict resource partitioning is that resources within an ecosystem (e.g. grass quality and quantity) are not static but vary both spatially and temporally. Digestibility (Crampton and Harris 1969) and protein content of grass (Mattson 1980) are negatively correlated with grass height. In addition, grass species

of the same height can differ in quality due to inter-specific differences in nutrient and lignin content. The spatial differences in grass availability and nutrient content make it possible for herbivores to partition resources at multiple scales (de Boer and Prins 1990). Many studies on savanna grazers have examined partitioning according to habitat choice (Bell 1970, Jarman, 1971, Jarman and Sinclair 1979); selection for plant height (Bell 1970, Jarman and Sinclair 1979, Owen-Smith 1985, Illius and Gordon 1987, Murray and Illius 2000, Arsenault and Owen-Smith 2008) and plant part (i.e. stem, leaf, sheath) or growth stage (Gwynne and Bell 1968, Bell 1970, Jarman and Sinclair 1979, Murray and Brown 1993, Murray and Illius 2000) but rarely their selection of individual plant species (but see Field 1972, Hansen et al. 1985, Sinclair 1985). Taking only grass height, growth stage and plant part eaten into account (as often done previously), may result in an underestimation of resource partitioning. These simple measures likely omit many nutritionally relevant differences among forage species, which herbivores detect and include in their diet selection.

Also, seasonal patterns of grass growth and maturation of the same species may introduce important temporal variability in forage quality and abundance (Grunow et al. 1980). This seasonal variation means that the way in which resources are partitioned and the scale at which they are partitioned (i.e. habitat or diet) may change seasonally (Arsenault and Owen-Smith 2002, Owen-Smith 2002). Although the effects of season on structuring herbivore communities have been discussed theoretically (Arsenault and Owen-Smith 2002, Owen-Smith 2002) it has rarely been examined in African savannas (but see Hansen et al. 1985; for temperate examples see: Hansen and Reid 1975, Olsen and Hansen 1977, Gordon and Illius 1989, Sietses et al. 2009).

Differences in body size (with potential allometric deviations in megaherbivores), digestive strategy, grass community composition and seasonal variation have thus all been suggested to impact the resource partitioning of savanna herbivores but have never all been addressed simultaneously in one integrative field study including several herbivores. Because all of these mechanisms underlying resource partitioning may interact and vary in importance in space and time, addressing them in separate studies done at different moments, on different individual species, and in different areas may yield misleading results. In this study we therefore investigated simultaneously the spatial and seasonal mechanisms of resource partition between six savanna herbivores: different-sized ruminants - impala, wildebeest and buffalo *Syncerus caffer*, and different-sized non-ruminants - warthog *Phacochoerus aethiopicus*, zebra *Equus burchellii*, and white rhinoceros, of which the last species is a megaherbivore. We explore the relative importance of body size, digestive strategy, the potential allometric deviation by megaherbivores, and season in explaining habitat and diet resource partitioning among these species.

Material and methods

Study area

Fieldwork for this study was carried out in the Corridor and Hluhluwe sections of Hluhluwe iMfolozi Park (HiP)

situated in central Zululand, South Africa (28°00'S and 28°26'S; 31°43'E and 32°09'E). HiP has an area of 89 665 ha and is surrounded by a game proof fence (Whateley and Porter 1983). The climate is characterized by annual daily maximum temperatures ranging between 13°C and 35°C and an average annual rainfall of 722 + 165 mm peaking between October and March (Jolles et al. 2006). HiP is hilly and ranges in altitude between 80 m and 450 m a.s.l. The dominant vegetation types occurring in the study area are *Acacia nilotica* – *Euclea divinorum* woodland and *Dichrostachys cinerea* – *A. nilotica* thickets in the lower lying areas; open thicket of *Acacia caffra* and *Acacia karoo* on the hill slopes and open *Themeda triandra* grasslands on the hill tops (Whateley and Porter 1983). The park has a high diversity of wildlife with the dominant grass consumers (grass is >50% of diet) being impala, warthog, wildebeest, zebra, buffalo and white rhino (Table 1).

Habitat selection

A total of 2282 independent herbivore (impala, warthog, wildebeest, zebra, buffalo and white rhino) observations were collected between July 2003 and June 2005. Driver transects, consisting of two routes both approximately 31 km, were performed for four consecutive days during each month. Observations were performed daily between 6:00 to 10:00 and 14:00 to 17:00. Driving speed was approximately 20 km h⁻¹ and the two routes were alternated between morning and afternoon so that they were equally driven at both times of the day. We searched for animals at a fixed distance away from the vehicle (100 m on either side). When an animal was sighted, it and the habitat type in which it occurred were identified. Habitats were classed as follows:

1. Grassland, vlei and encroached grassland (<25% woody plants).
2. Thicket, dense and impenetrable woody vegetation (>75% shrubs and/or trees).
3. Open woodland, trees with canopies not overlapping
4. Closed woodland, trees with overlapping canopies and grass beneath
5. Forest, no continuous grass cover
6. Watercourse, excluding those in forest.

Groups of animals were treated as individual observations (to avoid pseudoreplication) and only observations separate in time and space were considered independent. Because the dominant habitats are grassland and open woodland and because we searched for animals a fixed distance from the car

we are confident that differences in visibility between habitat types was not very large.

Herbivore selection of grass species and grass height

Between May 2004 and March 2005, a total of 2341 individual bite points from 161 animal feeding observations were measured. In the early morning and late afternoon (predominant feeding time of ungulates) we drove the same roads as used to make the animal habitat observations and searched for grazing individuals or groups within 100 m of the road. Once an individual or group was sighted feeding, detailed observations of the exact location where bites were taken were made (this observation was classified as a feeding observation). After the animal left the patch, the observer approached the patch on foot and searched for the freshly grazed grass i.e. individual bite points. Freshly grazed grass is identifiable as the bitten leaf/stem remains white while older grazed grass turns brown quickly. Grazed grasses were found and identified to the species level. However, due to difficulties of accurately identifying lawn grass species during the dry season (in some areas grass was grazed down to the ground and only stem was visible), lawn grasses were lumped into one category.

The height of the grass that the herbivore chose to graze was measured by determining the height of ungrazed leaves on grasses of the same species occurring in close proximity to the one grazed. Ungrazed grass measurements were performed on grasses of similar age and growth stage to the one grazed. Although we recognise that ungrazed plants might not have been chosen by the herbivore for a reason, we assumed that these grasses were not grazed due to chance and thus are not different to the grass actually grazed. At each feeding observation site we measured on average 10 (SD = 3.0) individual bite points (10 paired grazed and ungrazed grass species and heights) which were all at least 1 m apart. Larger sample sizes were achieved for buffalo during the dry season due to additional data collection in the course of a related project. Up to 150 bite points were sampled from 13 different herds observed between April and September 2004. For analysis, all grass height measurements were lumped into 10 cm categories.

Grass quality

Percentage nitrogen found in the green leaves of grasses was used as a measure of grass quality. Although we predominantly observed the herbivores to graze green leaves during both seasons, we acknowledge that for the bulk feeders diet quality will be overestimated (particularly in the dry season),

Table 1. Mammalian herbivore species and their relative densities occurring within Hluhluwe iMfolozi Park. Total herbivore numbers are based on a census carried out in 2004. Herbivore species are classified as grazer, intermediate feeder or browser according to Estes (1991). Body weights were obtained from Owen-Smith (1988).

Species	Scientific name	Digestive type and feeding style	Total numbers	Body mass (kg)	Density (no. ha ⁻¹)	Density (kg ha ⁻¹)
Impala	<i>Aepyceros melampus</i>	ruminant intermediate feeder	25563	40 – 63	0.285	14.682
Warthog	<i>Phacochoerus aethiopicus</i>	non-ruminant grazer	3284	58 – 80	0.037	2.527
Wildebeest	<i>Connochaetes taurinus</i>	ruminant grazer	3179	163 – 252	0.035	7.516
Zebra	<i>Equus burchelli</i>	non-ruminant grazer	3408	220 – 320	0.038	10.452
Buffalo	<i>Syncerus caffer</i>	ruminant grazer	3151	520 – 650	0.035	20.558
White rhino	<i>Ceratotherium simum</i>	non-ruminant grazer	1793	1600 – 2200	0.020	37.994

since they very likely also include stems and dry leaves in their forage due to their inability to feed very selectively. A total of 233 randomly sampled grass clumps of the most commonly grazed grass species were clipped at different locations within the study area during the dry and the wet season. Samples were dried and sorted. Green leaves were ground and analyzed, according to the macro-Kjeldahl digestion method, for organic nitrogen (Donkin et al. 1993).

Data analysis

Niche overlap was calculated using the formula of Pianka (1973)

$$O_{jk} = O_{kj} = \frac{\sum_i P_{ij} P_{ik}}{\sqrt{\sum_i P_{ij}^2 \sum_i P_{ik}^2}}$$

O_{jk} and O_{kj} are the degree of overlap between the species pairs and P_{ij} and P_{ik} are the proportions of the i th resource used by the j th and k th species respectively.

Overlap was calculated separately per season for habitat utilization, grass species and grass heights. The overall overlap values were calculated by taking the product of habitat, grass species and grass height overlap values as suggested in Pianka (1973). Overlap values range between 0 and 1, where 0 indicates no overlap and 1 indicates complete overlap.

For the purpose of the seasonal comparison, observations were classed into either the wet or dry season. Wet season observations included all measurements made between October and March and dry season observations were made between April and September. For investigations on the impact of digestive strategy on resource overlap, digestive strategies were categorized into two classes: concordant species pairs i.e. ruminant with ruminant or non-ruminant with non-ruminant, and discordant species pairs i.e. ruminant with non-ruminant.

All analyses were conducted in R (R Development Core Team 2009). Herbivore differences in habitat use and grass species grazed were compared using a chi-squared test. Grass height differences and grass quality utilization were compared between species and seasons using a one-way ANOVA and a Tukey post-hoc test. Seasonal differences

in overlap values were analyzed using a Wilcoxon matched pairs test. To test for the impact of digestive strategy and body mass on degree of resource overlap for habitat, grass height, grass species and overall overlap, we performed a linear regression on logistically transformed overlap values (i.e. $\log(O_{jk}/(1 - O_{jk}))$) (Royle and Dorazio 2008). Non-significant terms were eliminated, where appropriate, through backward elimination and the impact of this elimination on the model was tested using an ANOVA test. White rhino and their interactions with the other herbivore species were analysed separately (in the same way as described above) because they were a priori expected to behave very differently with regard to body size – food quality relations (see Introduction). In all cases, the interaction term (body mass $\times$ digestive strategy) was not significant ($p > 0.5$) and was excluded from the regression model.

Results

Habitat utilization

Although herbivore species showed subtle differences in habitat use (Fig. 1; dry season: $\chi^2 = 34.33$, DF = 20, $p = 0.02$; wet season: $\chi^2 = 80.46$, DF = 20, $p < 0.001$), all species overlapped extensively (0.97 average habitat overlap, Supplementary material Appendix 1A–B) in both seasons. The degree of habitat overlap between herbivore species was not different between the wet and the dry season (Wilcoxon matched pairs test, $Z = 0.40$, $n = 15$, $T = 53$, $p = 0.69$) nor was it related to digestive strategy (dry season overlap: $F_{(1,9)} = 0.16$, $p = 0.88$ (excluding white rhino); $F_{(1,3)} = 0.22$, $p = 0.85$ (white rhino only); wet season overlap $F_{(1,8)} = 1.80$, $p = 0.12$ (excluding white rhino); $F_{(1,3)} = 1.29$, $p = 0.33$ (white rhino only) or body mass (dry season overlap: $F_{(1,8)} = 0.25$, $p = 0.81$ (excluding white rhino); $F_{(1,4)} = 0.97$, $p = 0.40$ (white rhino only); wet season overlap $F_{(1,9)} = 1.26$, $p = 0.24$ (excluding white rhino); $F_{(1,4)} = 0.71$, $p = 0.53$ (white rhino only)) (Fig. 2A–B)

Grass height utilization

Different herbivores grazed different grass heights (Fig. 3, dry season: $F_{(5,1133)} = 90.83$, $p < 0.001$; wet season: $F_{(5,722)} = 56.89$, $p < 0.001$). For most species, grass height

Figure 1. Habitat use by six herbivore species during the dry and the wet seasons.

Figure 2. Seasonal comparison of overlap values and the difference in body mass and digestive strategy between the species pairs. (A) and (B) are habitat overlap for the dry and the wet seasons respectively, (C) and (D) are grass height overlap for the dry and wet seasons respectively, (E) and (F) are grass species overlap for the dry and wet seasons respectively and (G) and (H) are the overall overlap (product of habitat, grass height and grass species overlap values (Pianka 1973)) for the dry and wet seasons respectively. White rhino overlap values (grey symbols) were analyzed separately (Introduction – ruminant with ruminant or non-ruminant with non-ruminant (dots); and discordant – ruminant with non-ruminant (triangles)). Fitted curves are derived from the linear model with logistically transformed overlap values. A solid line represents a significant relationship between overlap and difference in body mass ($p < 0.05$) while a dashed line represents an almost significant relationship between overlap and difference in body mass ($p < 0.1$). Codes are as follows: I = impala, Wg = warthog, Wb = wildebeest, Z = zebra, B = buffalo, WR = white rhino.

preference changed between the wet and the dry seasons (Fig. 3, significant height class $\times$ season interaction, $F_{(5,1486)} = 23.40$, $p < 0.001$). Impala, zebra and buffalo all grazed longer grasses during the dry season and then swapped to shorter grasses during the wet season. White rhinos on the other hand grazed short grasses during the dry season and changed to relatively longer grasses during the wet season. Finally, wildebeest and warthog preferred grazing shorter grasses in both seasons and did not significantly alter their selected grass height (Tukey test $p > 0.05$). The combined

effect of these changes caused different species to converge in grass height utilized during the wet season whereas during the dry season grass height preference diverged (Fig. 3). This is further substantiated by the high average grass height overlap calculated between species during the wet season i.e. 0.80 average overlap, versus 0.63 average overlap calculated for the dry season (Supplementary material Appendix 1C–D). A Wilcoxon matched pairs test confirms that overlap values differ significantly between the wet and the dry seasons ($Z = 2.39$, $n = 15$, $T = 18$, $p = 0.02$).

Figure 3. Grass heights chosen (pre-graze height) by impala, warthog, wildebeest, zebra, buffalo and white rhino in HiP during the dry and the wet seasons.

Overlap in grass height preference of species pairs tended to increase as body mass differences decreased (Fig. 2C–D) (overlap between all species excluding white rhino: dry season: $F_{(1,9)} = -2.00$, $p = 0.08$; wet season: $F_{(1,9)} = -1.09$, $p = 0.31$). Digestive strategy had no significant impact on the relationship in either season (dry season: $F_{(1,8)} = 0.13$, $p = 0.90$; wet season: $F_{(1,8)} = -0.28$, $p = 0.79$).

White rhinos, on the other hand, showed the opposite trend to the smaller herbivores in the system. During the dry season white rhino were found to overlap most with the smaller species (i.e. impala, warthog and wildebeest; overlap = 0.90, 0.91 and 0.97 respectively) while overlap with the larger species (zebra and buffalo) was relatively low (overlap = 0.51 and 0.10 respectively). A weak positive relationship between body mass difference and overlap was found for the dry season (dry season: $F_{(1,4)} = 2.52$, $p = 0.09$, Fig. 2C, Supplementary material Appendix 1C) with digestive strategy having no impact on this relationship ($F_{(1,3)} = 0.90$, $p = 0.46$). While during the wet season all species overlapped to a high degree with white rhino (average overlap = 0.87) irrespective of body mass difference ($F_{(1,4)} = -0.53$, $p = 0.63$) or digestive strategy ($F_{(1,3)} = -0.424$, $p = 0.71$) (Fig. 2D, Supplementary material Appendix 1D).

Grass species utilization

Herbivores were found to graze different grass species to one another in each season (Table 2, herbivore $\times$ grass species association for the dry season: $\chi^2 = 1089.80$, $DF = 85$, $p < 0.001$; wet season: $\chi^2 = 493.82$, $DF = 70$, $p < 0.001$). Furthermore, all species were found to alter their diets between the wet and the dry season (grass species $\times$ season association for impala: $\chi^2 = 35.45$, $DF = 7$, $p < 0.001$; warthog: $\chi^2 = 38.74$, $DF = 8$, $p < 0.001$; wildebeest: $\chi^2 = 53.67$, $DF = 8$, $p < 0.001$; zebra: $\chi^2 = 57.80$, $DF = 14$, $p < 0.001$; buffalo: $\chi^2 = 286.97$, $DF = 16$, $p < 0.001$; white rhino: $\chi^2 = 83.80$, $DF = 8$, $p < 0.001$, Table 2). On average the overlap between species was relatively low (average dry season overlap = 0.61; average wet season overlap = 0.73, Supplementary material Appendix 1E–F) and seasonal comparisons in overlap between the species pairs were almost significantly different (Wilcoxon match pairs test $Z = 1.87$, $n = 15$, $T = 27$, $p = 0.06$). A significant negative relationship between overlap in grass species use and difference in body mass was found for the dry season (all except white rhino: $F_{(1,9)} = -3.00$, $p = 0.02$, Fig. 2E), while for the wet season no such trend was found (all species except white rhino: $F_{(1,9)} = -0.42$, $p = 0.69$, Fig. 2F). For

Table 2. Grass species composition (%) in the diet of six herbivore species during the (a) dry and the (b) wet seasons. Grasses consisting of greater than 5% of a species diet are included in the tables. Sample sizes are indicated in brackets below the herbivore species names.

(a) Dry season

Grass species	Impala (138)	Warthog (90)	Wildebeest (120)	Zebra (214)	Buffalo (995)	White rhino (59)
<i>Chloris gayana</i>	6	2	17	16	3	0
<i>Eragrostis curvula</i>	0	4	18	9	3	0
<i>Panicum maximum</i>	52	18	19	39	9	8
<i>Setaria sphacelata</i>	0	1	0	1	8	0
<i>Sorghum bicolor</i>	0	0	0	0	0	0
<i>Sporobolus africanus</i>	0	1	2	10	2	0
<i>Themeda triandra</i>	17	16	10	11	68	44
Other bunch grasses	0	1	1	2	6	0
Lawn grasses	25	57	33	12	2	48

(b) Wet season

Grass species	Impala (138)	Warthog (128)	Wildebeest (82)	Zebra (123)	Buffalo (104)	White rhino (150)
<i>Chloris gayana</i>	3	0	2	2	0	3
<i>Eragrostis curvula</i>	1	1	5	10	1	1
<i>Panicum maximum</i>	32	29	16	44	27	54
<i>Setaria sphacelata</i>	5	0	18	0	3	0
<i>Sorghum bicolor</i>	0	0	0	1	13	1
<i>Sporobolus africanus</i>	0	0	1	2	0	4
<i>Themeda triandra</i>	13	4	4	15	36	3
Other bunch grasses	1	0	0	12	0	5
Lawn grasses	45	66	54	15	20	30

both seasons digestive strategy had no impact on diet overlap between the species pairs (digestive strategy: dry season: $F_{(1,8)} = 0.76$, $p = 0.47$, wet season: $F_{(1,8)} = 0.39$, $p = 0.71$). Diet overlap of white rhino with the other species showed no relationship with body mass difference or digestive strategy in either season (body mass: dry season $F_{(1,3)} = -0.24$, $p = 0.83$; wet season: $F_{(1,4)} = 1.45$, $p = 0.24$; digestive strategy: dry season: $F_{(1,4)} = -0.33$, $p = 0.76$; wet season: $F_{(1,3)} = -0.10$, $p = 0.93$, Fig. 2E–F).

Multidimensional resource utilization

Multidimensional overlap in resource utilization was estimated by calculating the product of the overlap along all three niche dimensions (habitat, grass height and grass species) for each herbivore species pair (Pianka 1973) (Fig. 2G–H). During the dry season, niche overlap declined with the body mass difference between the species pairs ($F_{(1,9)} = -3.23$, $p = 0.01$). In contrast, during the wet season niche overlap between the species pairs did not depend on their size difference ($F_{(1,9)} = -1.00$, $p = 0.35$). Digestive strategy also had no impact on any of these relationships (digestive strategy: dry season: $F_{(1,8)} = 0.13$, $p = 0.90$, wet season: $F_{(1,8)} = 0.44$, $p = 0.67$).

No significant trends were found for species pairs that included white rhino (body mass: dry season: $F_{(1,4)} = 2.50$, $p = 0.09$; wet season: $F_{(1,3)} = 0.14$, $p = 0.90$; digestive strategy: dry season $F_{(1,3)} = 0.02$, $p = 0.99$, wet season $F_{(1,4)} = -0.37$, $p = 0.74$).

Diet quality

Herbivores consumed a lower quality diet during the dry season than during the wet season ($F_{(1,91.05)} = 1327.27$, $p < 0.001$, Fig. 4). Excluding white rhino, a significant

negative relationship was found between herbivore body mass and the nitrogen content of the diet during the dry season ($r^2 = 0.81$; $p = 0.04$, Fig. 4). On the other hand, white rhino consumed a diet of much higher quality than predicted from their size i.e. similar to impala during both seasons. During the wet season all herbivores consumed a diet of much higher quality and no trend between quality and body mass was observed ($r^2 = 0.22$; $p = 0.43$, Fig. 4).

Discussion

Many of the currently available studies on niche resource partitioning in African herbivores have been performed in the Serengeti-Mara ecosystem (Tanzania/Kenya). Most of these have found that resource partitioning between resident herbivores occurs primarily among habitats (Gwynne and Bell 1968, Bell 1970, McNaughton 1976, Jarman and Sinclair 1979). This is understandable as the Serengeti is very large (25 000 km²) and has relatively coarse landscape heterogeneity (plant abundance uniform over large areas) (Fryxell et al. 2005). In contrast, in our study area the overlap in habitat use was high between all grazer species in both the wet and the dry season. We attribute this difference to a contrast in size of reserve studied and degree and scale of habitat heterogeneity (Owen-Smith 2004, Fryxell et al. 2005, Cromsigt et al. 2009). HiP is a relatively small park (900 km²), surrounded by a fence (preventing migration) and has high heterogeneity between and within vegetation types (Whateley and Porter 1983, Cromsigt et al. 2009). Consequently, herbivore home ranges at HiP consist of many different habitat types and due to the high animal densities (10–30% higher than those typical for savanna reserves where migration is prevented) (Balfour and Howison 2002), overlap in habitat between herbivore species is unsurprisingly high.

Figure 4. Diet quality eaten by each of the six herbivore species during the dry season ($r^2 = 0.81$; $p = 0.04$) (filled symbols) and the wet season ($r^2 = 0.22$; $p = 0.43$) (open symbols), white rhino was not included in the regression. The herbivore digestive strategy: ruminant (circle) and non-ruminant (triangle) is also shown. Codes are as follows: I = Impala, Wg = warthog, Wb = wildebeest, Z = zebra, B = buffalo, WR = white rhino.

Where resource partitioning was not found to be strong at the level of habitats, it did appear to occur with regard to grass height and plant species utilized. Figure 5A–D give a conceptual summary of our results. These figures show how

different plant species (with different limits to their nutrient concentration and maximum height) and vegetation structure (dependent on season, grazing and plant species) form two main niche axes of plant biomass and plant quality (Fig. 5A–B) and how different herbivore species partition this niche space (Fig. 5C–D). Overall, we found that during the dry season all heights and grass qualities available were utilized (Fig. 5A, 5C), but that different herbivores used different fractions, leading to resource partitioning. The comparison of Fig. 5A–B and 5C–D suggests that coexistence of herbivores is facilitated by the co-occurrence of grasses with different growth form and quality. The small-scale coexistence of high quality short grazing “lawn grasses” like *Digitaria longiflora* and *Sporobolus nitens* with lower quality “bunch grasses” like *Sporobolus pyramydalis* and *Eragrostis curvula* is most likely mediated by the herbivores themselves (Cromsigt and Olff 2008, Waldram et al. 2008). In contrast, during the wet season the higher quality plant species were predominantly used by the herbivores while the low quality grasses were left untouched (Fig. 5B, 5D). An examination of Fig. 5C–D further illustrates this divergence of resource use (decreasing niche overlap) in the dry season versus convergence in the wet season.

Illius and Gordon (1993), Belovsky (1997) and Ritchie and Olff (1999) all proposed (but with different arguments) that co-existence of savanna herbivores is possible due to the exclusive use of a small portion of the niche space by each

Figure 5. Conceptual summary of results. (A) and (B) indicates the plant biomass and quality available to grazing herbivore species during the dry and wet seasons respectively (i.e. niche space available to herbivore species), while, (C) and (D) indicates the area of niche space occupied by the six herbivore species as well as how those species partition the available niche space during the dry and wet seasons respectively.

species (as predicted by body size differences). Generally, our results provide quantitative support for this hypothesis. However, the impala seems to be an exception in that it has no exclusive use of any portion of the niche space. Possibly the mixed feeding habits of impala (i.e. their ability to switch to browse when good quality grass runs out) allows them to escape competition with other grazer species. An alternative hypothesis is that impala seems not to have occurred in HiP in pre-western settlement times (at least in the late 1800s) and are thought to have been introduced only in the 1930s (Brooks and Macdonald 1983). Consequently, their lack of exclusive niche use could be evidence that impala did not evolve competitively with the other species in this area. Numerically, impala are by far the most abundant herbivores in the park (25 563 animals) while in terms of biomass they are third most abundant (Table 1). This together with the fact that a high proportion of their diet consists of grass (> 60% and 80% of their diets during the dry and wet seasons respectively) (Monro 1980, Botha and Stock 2005) brings into question the impact of impala (with respect to competition) on the other grazing herbivore species.

Demment and Van Soest (1985) and Prins and Olff (1996) suggest that if competition is important in structuring herbivore communities then body size differences should explain feeding differences between species. While others have argued instead that digestive strategy (Illius and Gordon 1992, Cromsigt et al. 2009) and breadth of incisor arcade (Illius and Gordon 1987, Arsenault and Owen-Smith 2008) may be better predictors for explaining resource partitioning. Our findings provide strong support for the role of body size in resource partitioning between grazing herbivores weighing less than 1000 kg. During the dry season, body mass is a strong predictor of resource overlap between the species pairs, where species more similar in size overlap to a higher degree. These allometric relationships are evident across both ruminant and non-ruminant herbivores. While allometric relations clearly play an important role in resource partitioning the role of digestive strategy cannot be completely discounted. Our sample size of species pairs with concordant ($n = 4$) and discordant ($n = 6$) digestive strategies, although high relative to other studies, was still too low to draw any strong conclusions from.

We confirmed our expectation from physiological arguments (see Introduction) that white rhino consume a much higher quality diet than would be predicted from their size. This high quality diet is realized by repeatedly cropping the same grazing lawns very short (Owen-Smith 1988, Shrader et al. 2006, Waldram et al. 2008) which seems to induce (pre-emptive) competition with much smaller short grass specialists (warthog and wildebeest) during the dry season (Waldram et al. 2008).

During the wet season, relations between body size difference and diet overlap were not found. All species consumed high quality diets resulting in higher average overlap in resource use. White rhinos were interesting as they changed their diet to utilize high quality grass of a range of heights.

Mechanisms of resource partitioning are assumed to be most strong during periods of food scarcity and for this reason most studies examine resource partitioning only during the dry season. However, the few studies that have performed seasonal comparisons have found contrasting results. Hansen et al. (1985) found no seasonal change in diet overlap among

Serengeti herbivores. In temperate habitats, most studies found diet overlap of herbivores to be higher during the summer than the winter (Hansen and Reid 1975, Olsen and Hansen 1977, Gordon and Illius 1989) (conforming to expectation) but Sietses et al. (2009) found the opposite trend (higher overlap in winter than summer). Our results reveal that overlap in resource use was lowest during the dry season (season of food shortage), thus suggesting that competition is greatest at that time of year.

In conclusion, we find predictable relations between fine-scaled resource overlap between species and their differences in body size, but only in the dry season when food is scarce. Resource partitioning between herbivores in the dry season (and hence coexistence) seemed to be facilitated by high local diversity of different grass species varying in growth form and quality (lawn versus bunch grasses). The megaherbivore species in our study (white rhino) however completely 'stepped out' of these relationships, possibly as a result of physiological limits to the ingesta retention time of forage in the gut.

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