3

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

Joris P. G. M. Cromsigt, Herbert H. T. Prins and Han Olff
Chapter 3

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 mechanisms 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, Cromsigt 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.

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

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 (ni) 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 \( i \) an \( j \), 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:

\[
\hat{W}_{i,s} = \frac{o_{i,s}}{\pi_i}
\]

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

\[
B_{i,s} = \frac{\hat{W}_{i,s}}{\sum_{i=1}^{12} \hat{W}_{i,s}}
\]

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.
Landscape use differences among large grazers

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.

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.

Acknowledgements

We would first of all like to thank the people that helped collecting the data for this study; M. te Beest and S. Khumalo. A special word of thanks goes to Emmanuel Buthelezi for his excellent work as a game guard, preventing potentially dangerous conflicts with large game on several occasions. Furthermore, we thank Ezemvelo KZN Wildlife for supporting this study, administratively as well as logistically; specifically S. van Rensburg, S. Nxumalo, J. Ngubane, D. Robertson, C. Reid, E. Smidt and S. Ras. This study has been financially supported by NWO-WOTRO (grant no. W84-501).
Landscape use differences among large grazers