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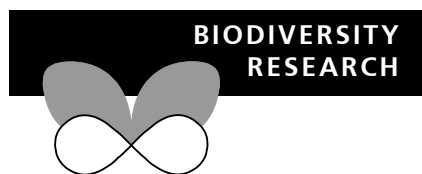
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Habitat heterogeneity as a driver of ungulate diversity and distribution patterns: interaction of body mass and digestive strategy

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ABSTRACT

Aim Classic island biogeographical theory predicts that reserves have to be large to conserve high biodiversity. Recent literature, however, suggests that habitat heterogeneity can counterbalance the effect of small reserve size. For savanna ungulates, body mass is said to drive habitat selection and facilitate species coexistence, where large species use a higher proportion of the landscape than smaller species, because a wider food quality tolerance allows them to use a higher diversity of habitat types. In this case, high habitat heterogeneity would facilitate diverse assemblages of different-sized ungulates. Digestive physiology should further modify this relationship, because non-ruminants have a wider diet tolerance than ruminants. We tested this hypothesis with an empirical dataset on distribution and habitat preference of different-sized African grazers.

Location Hluhluwe-iMfolozi Park, Republic of South Africa.

Methods We recorded herbivore dung and habitat type on 24 line transects varying between 4 and 11 km with a total length of 190 km to determine habitat selection and landscape distribution of six grazer species, three ruminants and three non-ruminants.

Results Larger ruminant grazers were more evenly distributed than smaller ruminants, had a more diverse use of habitats and used more low quality habitat. In contrast, non-ruminant grazers were more evenly distributed than similar-sized ruminants and body mass did not clearly influence diversity of habitat use and use of low quality habitat.

Main conclusions We confirm that body mass influences diversity of habitat use of large herbivores but digestive strategy potentially modifies this relationship. Hence, habitat heterogeneity might facilitate herbivore diversity in savanna ecosystems and high heterogeneity might counterbalance the effects of fragmentation and declining reserve size. Concluding, processes that homogenize the landscape, such as fire (mis)management and artificial waterholes, might be as threatening to biodiversity as landscape fragmentation, especially for smaller ruminant herbivores.

Keywords

Community ecology, grazing lawns, habitat heterogeneity, resource partitioning, savanna ungulate diversity, species–area relationships.

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INTRODUCTION

Biogeographical theory has played a major role in biodiversity conservation, specifically its application in reserve planning (Simberloff & Abele, 1976; Soulé & Terborgh, 1999). Island biogeography and the species–area relationship have been used to argue that bigger reserves are better suitable to maintain species

diversity (MacArthur & Wilson, 1967; Brashares *et al.*, 2001; Hansen & DeFries, 2007). However, Gurd (2006) showed, using island case studies, that small does not necessarily have to be bad, and that there are several examples of large islands losing a large proportion of their species and small islands maintaining complete species assemblages. Obviously, reserve size should not be the sole important characteristic in reserve selection. Recently,

more and more emphasis is given to the role of spatial heterogeneity in ecosystems (Fryxell *et al.*, 2005; Wang *et al.*, 2006). These studies suggest that spatial heterogeneity is a crucial reserve characteristic, independent from its size, for maintaining diverse species assemblages and buffering against temporal variability, such as a changing climate. In fact, spatial heterogeneity, in terms of habitat heterogeneity, might even override classic species–area relationships if habitat heterogeneity is uncorrelated to reserve area (Báldi, 2008).

A clear showcase of the increasing emphasis on spatial heterogeneity in biodiversity conservation has been the adoption of the so-called 'heterogeneity paradigm' in the management of grazing systems (Du Toit & Cumming, 1999; Fuhlendorf & Engle, 2001; Du Toit *et al.*, 2003; Kroger & 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 the lack of migration opportunities (Owen-Smith, 2004; Fryxell *et al.*, 2005). One of the challenges of this new paradigm is to come up with operational definitions of heterogeneity that can be used to set management targets, based on clear ecological theory (Gillson & Duffin, 2007).

Ecological theory has linked heterogeneity to savanna herbivore diversity pattern through the role of spatial resource partitioning as a condition for species coexistence (Ritchie & Olff, 1999; Wilmshurst *et al.*, 2000; Arsenault & Owen-Smith, 2002; Cromsigt & Olff, 2006). Spatial resource partitioning can occur at multiple scales, from plant species and the feeding patch level to larger landscape scales (e.g. Senft *et al.*, 1987). At the landscape scale, Du Toit & Owen-Smith (1989) explored how body mass differences among browsers affect their habitat selection and landscape use. They hypothesized that the wider food quality tolerance of larger species (Bell, 1971; Jarman, 1974; Gordon & Illius, 1996) allows them to use a larger proportion of the landscape by using a higher diversity of habitats, including habitats that are of too low resource quality for the smaller species. Hence, they showed that larger browsers are more evenly distributed over the landscape than smaller ones. This provides a mechanism through which landscapes with higher habitat diversity can support a higher diversity of different-sized herbivore species, and an operational definition of heterogeneity (see also Du Toit & Cumming, 1999; Ritchie & Olff, 1999; Redfern *et al.*, 2006).

We therefore need to generalize the idea of Du Toit & Owen-Smith (1989) on the relation between body size and habitat diversity, and explore if it also holds for species with other feeding and digestive strategies. The ruminant browsers that Du Toit & Owen-Smith (1989) investigated are only a small subset of the functional diversity found in savanna herbivores. Several mammalian savanna herbivores include grass as a main component in their diet, a feeding group that we call grazers. In addition, some species have a non-ruminant digestive strategy, which has important potential consequences for diet and habitat selection. In contrast to ruminants, non-ruminants can compensate for a less efficient nutrient extraction with a faster throughput rate

especially on low-quality foods, allowing them to eat more of such food (Duncan *et al.*, 1990). The net result is that non-ruminants are more effective in processing low-quality food (high fibre content) than ruminants (Demment & Van Soest, 1985; Owen-Smith, 1988; Duncan *et al.*, 1990; Illius & Gordon, 1992). Due to this wider food-quality tolerance, we hypothesize that non-ruminants can use a wider variety of habitats than similar-sized ruminants, including habitats that are of too low resource quality for similar-sized ruminants. We suggest that this potentially dampens the key role of body size that was hypothesized for ruminants.

We investigate the proposed interaction between body size and digestive strategy in a large-scale survey of the habitat use of ruminant and non-ruminant grazers in a heterogeneous savanna reserve in South Africa. We recorded the presence of ruminant and non-ruminant grazers in different habitat types from their dung, by walking transects with a total length of 190 km that resulted in close to 20,000 species–habitat associations. We show that body mass influences the diversity of habitat use more strongly in ruminants than in non-ruminants and that non-ruminants are more widely distributed over the landscape than similar-sized ruminants. Based on these results we discuss the importance of spatial heterogeneity in savanna reserves in relation to reserve size and potential impact of processes that homogenize the landscape.

METHODS

Study site

The study was performed in the Hluhluwe–iMfolozi Park (HiP); 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 & Porter, 1983; Owen-Smith, 2004). This heterogeneity is explained by strong local and regional gradients in elevation and rainfall, strong geological and soil heterogeneity and by local mosaics in vegetation structure ranging from open grassland to closed woodland, driven by the interplay of fire and herbivory in the park (Archibald *et al.*, 2005; Cromsigt & Olff, 2008). Mean annual rainfall ranges from 700–1000 mm rainfall per year in the hilly northern part of the reserve to 650 mm in the southern basin (Owen-Smith, 2004).

Grazer distribution

During the end of the dry season, 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 in length (8 km on average), with a total length of 190 km. We sampled at the end of the dry season because it reflects the period with strongest resource scarcity and, hence, potentially largest differences in grazer resource partitioning. Transects were evenly distributed over the reserve, covering all main vegetation types and elevation and rainfall gradients (Fig. 1). The most southern end of the park

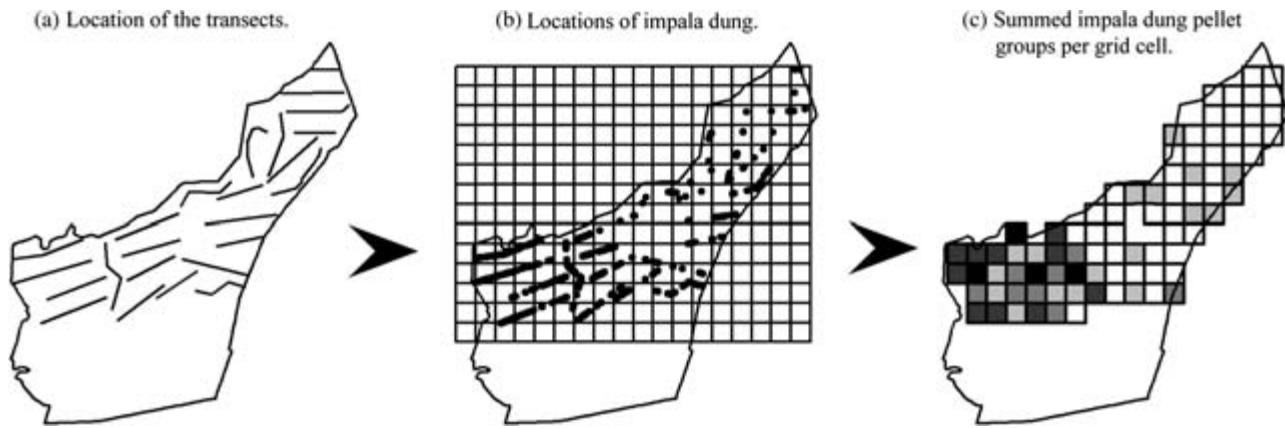


Figure 1 Process of joining a 2.5×2.5 km grid with the dung count point data using ArcMap 9.0 (ESRI, 2004). (a) Outline of Hluhluwe-iMfolozi Park showing the position of the 24 transects. (b) Locations where we found dung of a species (in this case impala), overlaid with a grid of 2.5×2.5 km cells. (c)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

was excluded from the study, due to access restrictions for researchers (wilderness concept). The transects were walked with a team of two well-trained observers, allowing reliable identification of species based on dung, that continuously counted the number of dung pellet groups per species on and within 1 m on each side of the transect. The number of dung pellet groups per species was recorded per 5 m plot along a transect. We recorded dung of the six most frequently observed grazer species in the park, consisting of three ruminant grazers (impala *Aepyceros melampus*, blue wildebeest *Connochaetes taurinus* and African buffalo *Syncerus caffer*) and three non-ruminant grazers (common warthog *Phacochoerus africanus*, plains zebra *Equus quagga* and white rhino *Ceratotherium simum*). 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 m from the transect centre. Wildebeest, buffalo, zebra and rhino are strict grazers (Owen-Smith, 1988; Hofmann, 1989), as is warthog in Hluhluwe-iMfolozi Park (> 80% grass in diet, Botha & Stock, 2005). Though impala is regarded as a mixed feeder (Hofmann, 1989), in HiP it predominantly grazes for much of the year and it was, therefore, also included in this study (> 70% grass in diet (Botha & Stock, 2005); see also Arsenaault & Owen-Smith, 2008). Other less common grazer species, such as waterbuck (*Kobus ellipsiprymnus*), occur in HiP, but we were not able to collect sufficient data to include them in this study. An important assumption for our study is that dung of all species is equally persistent and visible on transects. Equal visibility was greatly enhanced because all tall grass and shrubs were cut on transect strips before the start of this study. Our assumption of equal persistence is supported by an experimental study in HiP of disappearance rate of dung of all species in this study. Jacobs (2002) showed that during the dry season disappearance rate of dung did not clearly differ between species and dung of all species was still perfectly recognizable after more than 2 months of monitoring (Jacobs, 2002).

Habitat types

Every 100 m along a transect we recorded the dominant habitat type within a circle with 500 m radius, classified in seven types: grassland, thicket, open woodland, closed woodland, riverine forest, gallery forest and watercourses (Table 1). We measured grazer habitat resource quality independently from habitat type. In HiP, as in other African savanna grasslands, grazing lawns (or hot-spots) stand out as patches of very high resource quality, characterized as areas dominated by grazing-tolerant stoloniferous grass species (Archibald *et al.*, 2005; Cromsigt & Olf, 2008). Across Africa, 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 (Serengeti National Park: McNaughton, 1979, 1984; Ruess *et al.*, 1983; Kruger National Park: Grant & Scholes, 2006). All habitat types in Table 1 (except gallery forest and water courses which have no grass layer) can be found either with or without grazing lawns. We defined habitat resource quality according to two classes; grazing lawn present (high resource quality) and grazing lawn absent (low resource quality). We classified all seven habitats as high (with grazing lawns) or low (without grazing lawns) resource quality habitats, resulting in a total of 12 habitat classes for calculating habitat selection indices. Similar to the dung counts, we recorded grazing lawn presence every 5 m along the transect. We defined grazing lawn as present when lawn grass species dominated (> 75%) a 5-m plot and extended for several metres away on both sites of a transect (at least 5 m), 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 herbivore species were distributed

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.

over the landscape. We overlaid the dung count data with a grid of 2.5 × 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 metres that a grid cell was intersected by transects to get a density estimate (number of dung pellet groups per metre) for each grid cell hereby correcting for the sampling effort. Finally we standardized the densities for each species by dividing the density per grid cell by the maximum density found per species over all cells. We only calculated the relative density for grid cells that were intersected by minimally 500 m transect.

As a measure for the degree of spatial autocorrelation (clustering) per species we determined Moran's *I* (Moran, 1948) 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 (plots on the transects), *X_i* is the dung count of the species on location *i*, *X_j* the dung count on a different location *j*, \bar{X} is the grand mean of the dung count and *W_{i,j}* is the inverse Euclidian distance between the two locations *i* and *j*. The resulting index *I* ranges between -1 and 1, from a highly dispersed (-1) to a highly clustered distribution (+1). We expect that smaller ruminants are 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 of the same body mass 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

As a measure of habitat selection for the different grazer species we calculated Manly's standardized selection ratios (Manly *et al.*, 2002). We first calculated resource selection functions as the proportion of available habitat units (5 m 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 habitat *i* among all sampled habitat units. 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 interpreted as the probability that species *s* selects habitat *i* if all habitats would be equally available.

Per species we calculated the diversity of habitat use as Shannon–Wiener diversity index (Pielou, 1975; Du Toit & 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 habitat with high resource quality that was selected by each species.

RESULTS

Species distributions

The six grazer species were differently distributed over the landscape (Fig. 2). The smallest ruminant, impala, was highly concentrated in the south-western part of the park. The intermediate-sized wildebeest was slightly more dispersed over the landscape, with concentrations in the south-west, similar to impala but also high local abundance in the north-east. The largest ruminant, buffalo, and all three 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 changed from strongly right-skewed for the two smallest ruminants to more symmetric for buffalo, while this distribution changed much less with body mass for the non-ruminants (Fig. 3).

We tested these conclusions statistically through calculating Moran's *I* values. 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. 4a),

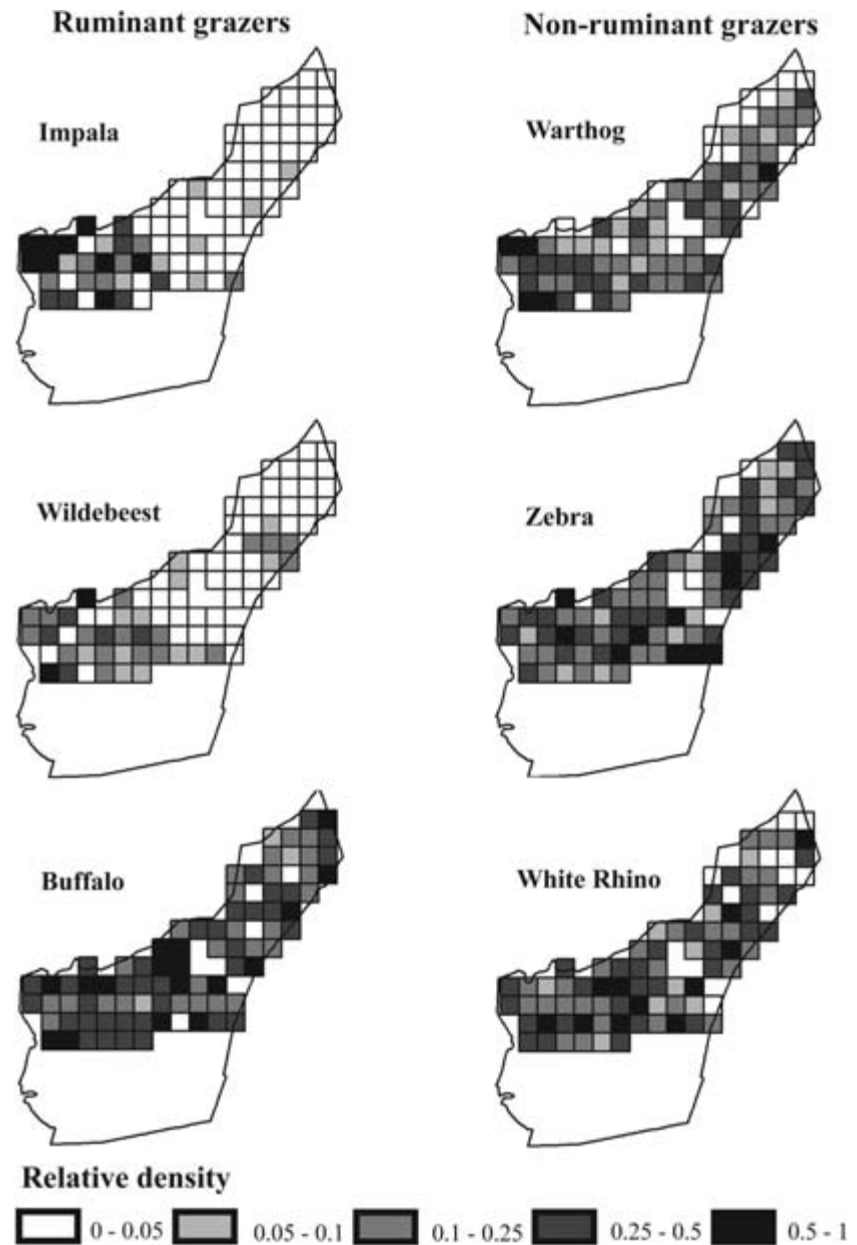


Figure 2 Distribution of ruminant and non-ruminant grazers in Hluhluwe-iMfolozi Park. Distribution is expressed as relative densities (proportion of maximum observed density) of dung pellet groups for 6 grazer species in 2.5×2.5 km grid cells.

indicating that smaller ruminant grazers are more clustered in the landscape than larger grazers. Among the non-ruminants, warthog distribution was clustered ($P < 0.01$) but much less than the ruminant grazer with comparable body mass, impala. Zebra and white rhino spatial distributions were not significantly clustered ($P > 0.05$).

Habitat selection

The diversity of habitat use (calculated as the Shannon–Wiener index of diversity (H') of habitats used) strongly increased with increasing body mass for the ruminant grazers (Fig. 4b) from 0.7 for impala to 1.05 for buffalo. In the non-ruminants, warthog and zebra had much more diverse habitat use than the similar-sized ruminants impala and wildebeest, respectively. On the

other hand, white rhino had a lower diversity of habitat use than expected from the ruminant pattern, as it was similar to buffalo, which is less than half its size. As a result, diversity of habitat use did not increase with body mass in the non-ruminants (Fig. 4b). The low diversity of habitat use in the smaller ruminants (impala and wildebeest) coincided with a higher selection for habitats containing grazing lawns than all other species (Fig. 4c). The much lower preference of the largest ruminant (buffalo) for grazing lawns was not found in the non-ruminants; white rhino had a similar preference for lawns as zebra and warthog.

DISCUSSION

We found that ruminant grazing species were more evenly distributed over the landscape with increasing body mass

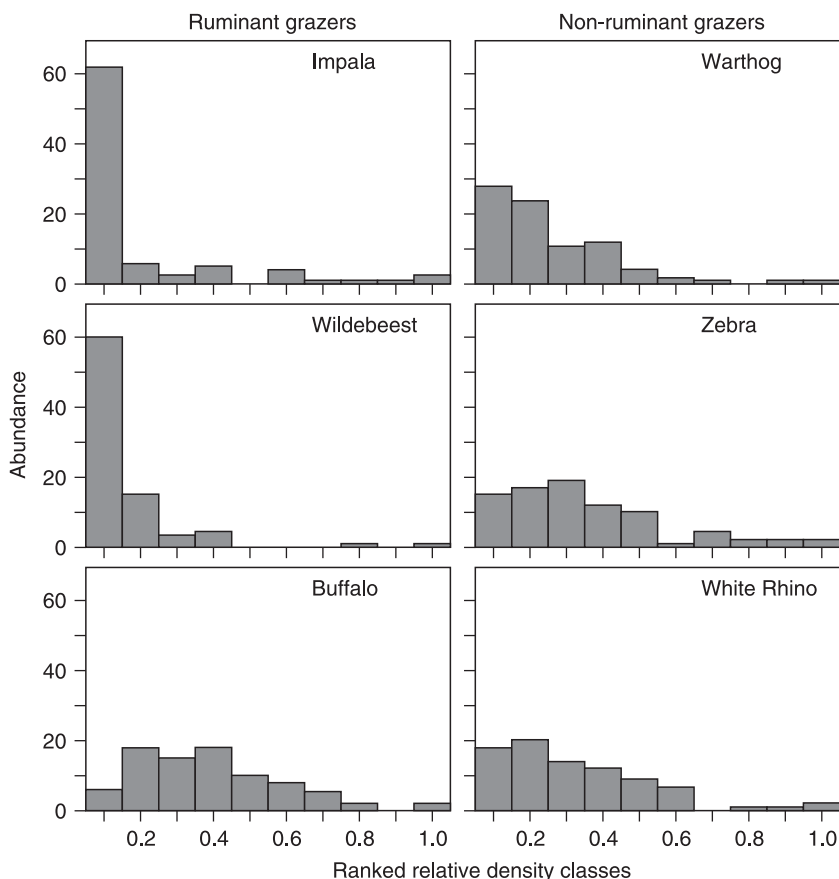


Figure 3 Rank–abundance plots of the relative densities that are displayed in Fig. 2. Bars show the number of 2.5×2.5 km grid cells with relative densities falling within the classes that are defined on the x-axis.

(Figs 2, 3 and 4a). Also, the diversity of habitat use of ruminant grazers strongly increased with increasing body mass, as Du Toit & 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 habitat with lower resource quality (habitat without lawn cover) by larger species (Fig. 4c). However, as hypothesized, the relationship between body mass and habitat diversity was much less clear for non-ruminant grazers. Only the smallest non-ruminant, warthog, was significantly clustered in the landscape, but much less strongly than impala, the similar-sized ruminant (Fig. 4a). 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 & Owen-Smith (1989) thus seems to hold for ruminant grazers as well (see also Redfern *et al.*, 2006), though the relationship is less clear for non-ruminant grazers. The smaller and intermediate-sized non-ruminants, warthog and zebra, had a more much more diverse use of habitats than similar-sized ruminants.

In this study we used dung counts as a method to estimate habitat selection rather than direct observations. Though herbivores do not necessarily always defecate where they graze, i.e. in the actual feeding patch, they generally defecate in the same locality as where they forage. In fact, increased nutrient input through dung is one of the main mechanisms behind positive consumer-resource feedbacks where grazers facilitate their food availability (Ruess *et al.*, 1983; Cromsigt & Olff, 2008).

Hence, we argue that dung counts are probably not the best method for looking at feeding patch selection, but provide a reliable estimate for habitat utilization of large grazers. We believe it is preferable above observational counts with its potential large biases, especially for the smaller size classes and in low-visibility habitats (Caro, 1999; Barnes, 2001). As our study shows, unbiased observation of herbivores of different size and occurring in open as well as closed habitats is crucial to understand actual differences in their distribution patterns.

Clearly, factors besides food resource availability can drive herbivore distribution patterns. Redfern *et al.* (2003) showed for Kruger National Park that water availability can influence herbivore distribution on a landscape scale. Perennial water sources are, however, widely available in HiP, and, therefore, water is not expected to limit grazer landscape distribution in HiP to the extent it does in Kruger National Park. Predation is another important factor that can influence herbivore distribution. Hopcraft *et al.* (2005) recently suggested that lions focus on areas with high prey ‘catchability’ rather than high prey abundance, explaining why herbivores often avoid dense-cover habitats (Sinclair, 1985; Prins & 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 too risky for smaller species. Consequently, differences in predation pressure and habitat resource quality can cause the same body mass–herbivore

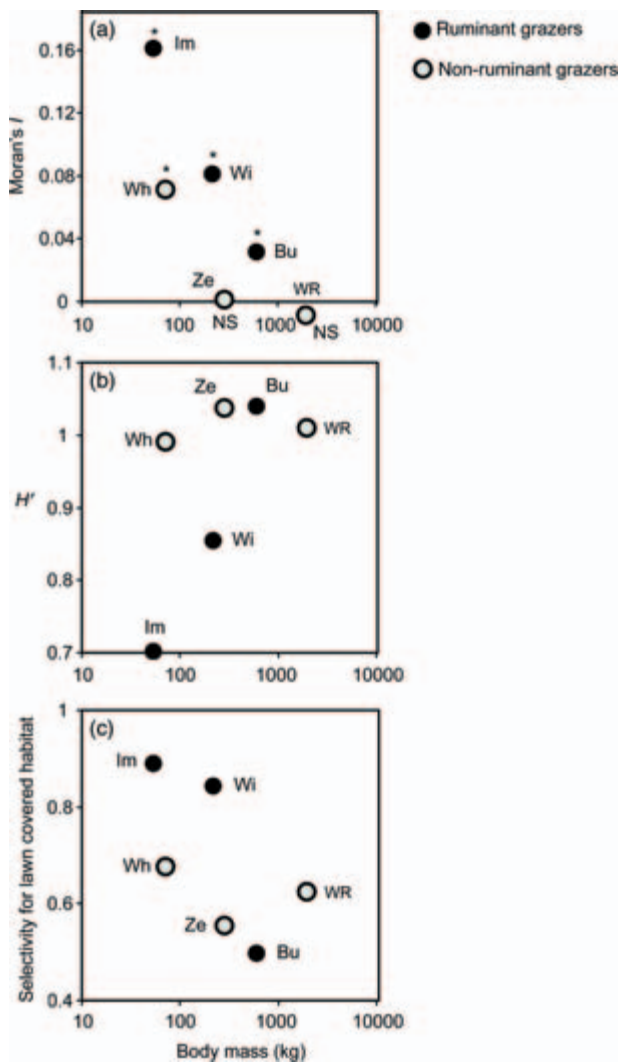


Figure 4 (a) Moran's I values for ruminant (left) and non-ruminant (right) grazers against their body mass. Ruminant grazers; IM (impala) $I = 0.16$, $Z = 12.4$, WI (wildebeest) $I = 0.08$, $Z = 7.4$, BU (buffalo) $I = 0.03$, $Z = 3.1$. Non-ruminant grazers; WH (warthog) $I = 0.07$, $Z = 6.0$, ZE (zebra) $I = 0.00$, $Z = 1.5$, 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 auto correlated and significantly different from a random distribution with $P < 0.01$ (in our case clustered because for all species $I > 0$). (b) 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. (c) 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. In all graphs body mass represents the average over male and female body mass as given by Owen-Smith (1988).

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 resource quality and predation risk influences large herbivore distributions.

The increase in diversity of habitat use with body size that we observed for grazers was much higher than observed for browsers in the study of Du Toit & Owen-Smith (1989). The diversity of habitats used by grazers in our study increased 50% as body mass increased 10-fold. In contrast Du Toit & Owen-Smith (1989) found for browsers in Kruger National Park 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 vs 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 National Park and HiP. If some of the 14 habitat types are very dominant in Kruger National Park and others are only sparsely available in a few locations, this would decrease the potential diversity of habitat that can be selected by an individual of a certain 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 form a finer-grained mosaic than in the much larger Kruger National Park and all habitats are present in every part of the reserve. This makes it easier for species to switch between habitat types on a daily foraging routine.

The previous paragraph illustrates that savannas are a good example of systems where habitat heterogeneity is not necessarily correlated with reserve area. As mentioned in the introduction, in this case the effects of habitat heterogeneity can override classic species–area relationships and result in high species diversity in relatively small reserves (Báldi, 2008). Besides species richness, such heterogeneity might also facilitate high density of the different grazer species in savanna systems. Wang *et al.* (2006) show how spatial resource heterogeneity can counterbalance destabilizing effects of temporal heterogeneity on large herbivore population dynamics by weakening density-dependent feedbacks and, hence, increase long-term densities. Interestingly, our study system has a fairly similar grazer biomass density as the Serengeti ecosystem (90 vs 110 kg per ha respectively, Cromsigt, 2006), despite being more than 25 times smaller. In addition, a large part of the grazer biomass in the Serengeti is migratory. In terms of sedentary grazers, the biomass density is arguably higher in HiP than in the Serengeti. As mentioned, HiP offers herbivores high habitat heterogeneity. Fryxell *et al.* (2005) argued, using Serengeti as an example, that protected areas have to be sufficiently large so that animals can migrate between key habitats or have to be very heterogeneous (i.e. low spatial autocorrelation in resource availability) to allow populations to persist in smaller areas. Serengeti and HiP might represent both extremes of this reserve extent versus heterogeneity continuum. The Serengeti ecosystem exhibits a very high spatial autocorrelation in resource distribution

(Fryxell *et al.*, 2005), where short and tall grasslands are large and very far apart. In contrast this spatial autocorrelation in HiP is much weaker, and the bunch and lawn grasslands are only few kilometres or less apart (Cromsigt, 2006). This fine-scale heterogeneity in grassland types might be responsible for maintaining the stable, high density populations of diverse grazers in HiP, as has previously been suggested by Owen-Smith (2004).

We defined habitat resource quality through the occurrence of grazing lawns. This enabled us to relate diversity of habitat use to a measure of resource quality of a habitat that was relatively quick and easy to measure. Our data suggest that diversity of habitat use is indeed related to habitat resource quality as defined by presence of lawns, specifically for ruminant grazers (as was hypothesized but not tested by Du Toit & Owen-Smith, 1989 for browsers). While we realize that we used a fairly rough classification of habitat quality, grazing lawns or hot-spots are increasingly recognized as key resource areas of savanna grassland systems (Illius & O'Connor, 2000; Grant & Scholes, 2006; Verweij *et al.*, 2006; Archibald, 2008). Understanding the mechanisms that create lawn distribution patterns over the landscape might prove crucial for the long-term conservation of especially, small- to medium-sized ruminant grazers (Verweij *et al.*, 2006). In this respect, it is important to consider that processes that homogenize landscapes might pose at least as big a threat to biodiversity conservation as fragmentation of the landscape. Such homogenizing processes in grazing systems include fire (mis)management, artificial waterholes and supplementary feeding (Owen-Smith, 1996; Archibald *et al.*, 2005; Kroger & Rogers, 2005). Results from this study suggest that such homogenizing processes might form a specific threat to the smaller species, and, importantly, more to ruminant than to non-ruminant grazers because they seem to rely more on specific habitats or resource hot-spots in the landscape. Hence, we join the recent plea that management should increasingly be familiar with the role of spatial heterogeneity and patchiness in savannas (Kroger & Rogers, 2005).

Concluding, our results suggest that habitat heterogeneity, specifically diversity of habitat resource quality, plays a role in resource partitioning at the landscape scale among different-sized grazer species. In contrast with non-ruminants and large ruminants, the small to medium-sized ruminant grazers were more concentrated in the landscape and used less diverse habitat types. The results of our study confirm the need to include the concept of heterogeneity in the application of island biogeographical theory to conservation, specifically when habitat heterogeneity is uncorrelated with reserve size (Baldi, 2008). Differences in heterogeneity might explain the difference in species extinction on the different islands that Gurd (2006) discussed. In terms of the conservation of grazing systems, high spatial heterogeneity, in terms of high spatial variation in habitats with different resource quality, might indeed to some extent counterbalance the size of reserves. As the 'heterogeneity paradigm' suggests, this should be considered in future reserve planning, especially in the light of climatic change, and emphasizes a special role for some of the smaller, but highly heterogeneous reserves, such as Hluhluwe-iMfolozi Park.

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