

6

Dynamics of grazing lawn formation: an experimental test of the role of scale-dependent processes

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Nonhlahla, you've been a longtime SABRE member from 2002-2006. I always greatly enjoyed working with you. Behind the sometimes tough look was always a fantastic smile. Thanks for this and many fun conversations. I hope I will not meet you at some South African highway in your new position as a police officer...

Abstract

Though the concept of grazing lawns has already been developed in the early 1970s the mechanisms and conditions that create these lawns are still poorly understood. There is a need for more experimental studies in natural environments. Past studies have suggested that an increased nutrient input induces lawn formation in combination with grazing by unselective herbivores. We argue that these ideas lack a spatial component. Using recent ideas that link self-organized patchiness to catastrophic shifts, we hypothesize that an increased nutrient input indeed promotes grazing lawn development but only after a disturbance above a certain threshold spatial resolution. We developed an experiment to test this hypothesis. In a diverse South African savanna we mowed short grass patches with different spatial resolution in formerly tall grassland and increased nutrient input of half of these plots. We stopped the treatments after two years, but continued monitoring the vegetation height and composition during the following two years. Grazing kept the vegetation short in the coarser, fertilized plots, while the grasses grew out toward their initial height in the finer grained and unfertilized plots. Moreover, stoloniferous lawn-forming grasses strongly increased in cover in the plots with an increased nutrient input but only above a certain threshold resolution. These insights provide a new spatial dimension to the concept of grazing lawn formation, and help to understand how vegetation heterogeneity in grassland ecosystems is created and maintained by herbivores.

Introduction

The grazing lawn concept was first formulated in the early 1970s (Bell 1971), after which McNaughton (1984) formally defined and further developed it as the co-evolution between herds of grazing animals and plant form. Central to this idea is the positive feedback between herbivore consumption and the availability of their food. Several studies suggested that herbivores can increase both the quality of their food by enhancing the nitrogen content of the grasses they graze (McNaughton 1979; Coppock et al. 1983a; Detling and Painter 1983; Ruess et al. 1983) and the availability of their food by accelerating primary production of the grazed vegetation (McNaughton 1976; Cargill and Jefferies 1984; Hik and Jefferies 1990; Ruess et al. 1997). Furthermore, grazers regularly influence plant community composition (Augustine and McNaughton 1998; Olff and Ritchie 1998), and induce changes in nutrient cycling (Holland and Detling 1990; McNaughton et al. 1997; Bakker et al. 2004), which both may affect plant productivity and quality.

The importance of grazing lawns in plant-herbivore interactions is widely recognized in systems ranging from tropical savannas to arctic tundra (Bell 1971; Coppock et al. 1983b; McNaughton 1984; Person et al. 2003). Studies in these systems generally focused on the role of lawns in the temporal dynamics of herbivore populations (Wilmshurst et al. 1999; Person et al. 2003). However, grazing lawns are also a critical component of small-scale spatial heterogeneity in grasslands, characterized by alternating patches of short and tall grass (Owen-Smith 2004). Next to the influence on the foraging behavior of large herbivores (Hester and Baillie 1998; Hester et al. 1999; Wallis de Vries et al. 1999) this small-scale heterogeneity might also mediate resource partitioning among large grazers (Ritchie and Olff 1999, Cromsigt and Olff in press) and hence contribute to their coexistence. Cromsigt and Olff (in press) indeed showed experimentally that differences in the size of short grass patches might promote spatial resource partitioning amongst large African grazers.

While the importance of grazing lawns in temporal and spatial dynamics of herbivore communities is increasingly recognized, we know much less about the mechanisms and conditions that create these lawns. Some work has suggested that grazing lawn distribution on a landscape scale is largely shaped by spatial differences in abiotic factors, like soil types, precipitation, altitude and fire (Bell 1971; McNaughton 1983a; East 1984; Archibald et al. 2005). An increased nutrient input has been argued to induce lawn formation on a more local scale (Ruess and McNaughton 1984; Day and Detling 1990). When nutrient availability is high lawn grasses show compensatory growth in response to grazing (McNaughton 1983b; Augustine and McNaughton 1998). Moreover, Huisman and Olff (1998) show that grazing by unselective herbivores may prevent bunch grasses from out shading the shorter lawn species. While unselective grazing of bunch grasses combined with an increased nutrient input might be essential processes that explain how lawn grasses replace bunch grasses, these mechanisms do not clearly link processes to spatial

scale making it difficult to explain observed small-scale spatial patterns of lawn and bunch grass patches.

Recent ideas that link self-organized patchiness to catastrophic shifts in vegetation patterns (HilleRisLambers et al. 2001; Rietkerk et al. 2004) provide a useful framework for thinking about how grazing can induce small-scale lawn-bunch mosaics. These studies suggest that the crucial positive feedback control between consumers and resources that underlies shifts between vegetation patterns is scale-dependent. In this study, we hypothesize that such a scale-dependent feedback plays an important role in grazing lawn formation and in the creation of lawn-bunch mosaics in savanna grasslands. We suggest that an increased nutrient input induces a positive feedback between grazing and grazing lawn formation, but only after a disturbance coarser than a certain threshold spatial resolution. Cromsigt and Olff (in press) showed that grazing intensity disproportionately increased if short grass patches were less fragmented (coarser resolution). Following this result we suggest that at resolutions finer than a threshold resolution grazing intensity is too low for a positive feedback to come into force, despite an increased nutrient input. Disturbances, ranging from local to landscape scale, typically structure savanna systems (Van Langevelde et al. 2003, Gillson 2004). On the local-scale of grassland mosaic formation we can identify fine-scale disturbances, such as small termite mounds, and more coarse scale disturbances, such as rhino middens and wallows (Fig. 1). These coarse-scale disturbances are typically caused by megaherbivores, like white and black rhino or hippo (Owen-Smith 1988, Cumming and Cumming 2003, Hobbs and Searl 2005). Both fine and

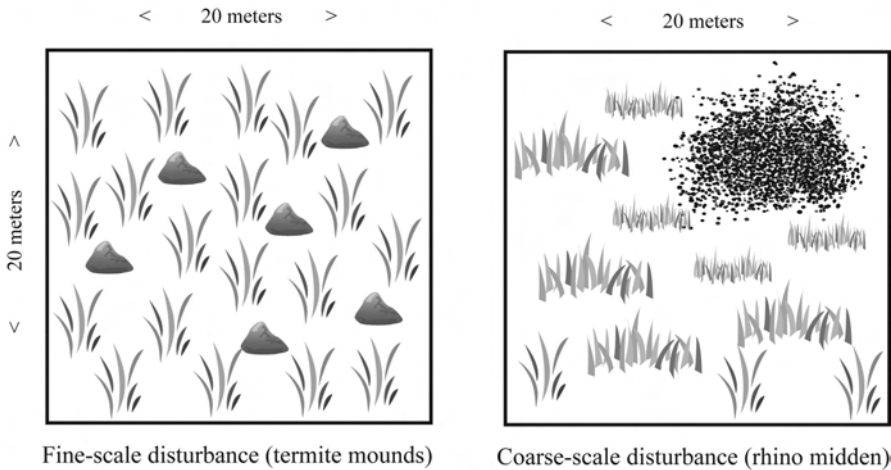


Figure 1 - Examples of fine scale (small termite mounds on the left-hand side) and coarse scale (rhino midden) disturbances in savanna grassland systems. The disturbances are characterized by locally opening up the bunch grass vegetation and increasing nutrient input. Grazing intensity, however, is too low in the fine scale disturbance plots to keep bunch grass short, in contrast with the coarser scale disturbance, where bunch grass is kept short around the disturbance.

coarse scale disturbances open up the bunch grassland and for a prolonged period of time trample and graze down the bunch vegetation. Moreover, both disturbances are also characterized by an increased nutrient input, local nutrient concentration in case of termites (Jones 1990) and increased urine and dung input in case of megaherbivore middens and wallows. However, we hypothesize that only at the coarser scale resolution grazing pressure will be high enough to promote consumer-resource feedback that leads to grazing lawn development.

We tested this idea in Hluhluwe-iMfolozi Park, South Africa by creating disturbances with different spatial resolution by regularly mowing plots of different sizes in bush-encroached, tall grass vegetation and enhancing the nutrient input to half of these plots with artificial fertilizer. We followed the vegetation development over more than 3 years to see whether an increased nutrient input induced lawn formation and to what extent this process depended on the spatial scale of disturbed patches.

Methods

Study site

The study was performed in Hluhluwe-iMfolozi Park (HiP), a small (90,000 ha) but diverse protected area in Kwazulu-Natal, South Africa. This reserve is situated in the southern African savanna biome, with vegetation types ranging from open grasslands to closed *Acacia* and broad-leaved woodlands (Whateley and Porter 1983). The mean annual rainfall depends on altitude, ranging from 985 mm in the high altitude regions to 650 mm in the lower areas and mainly falls between October and March. Daily maximum temperatures range from 13 °C to 35 °C. The reserve is of strong conservation importance because it hosts a rich and complete set of indigenous large herbivores and carnivores.

The park is characterized by highly heterogeneous grasslands, in which tall bunch grass (tussock forming) communities of *Sporobolus pyramidalis*, *Eragrostis curvula* and *Themeda triandra* are interspersed with short lawn-forming (stoloniferous) communities of *Digitaria longiflora*, *Urochloa mosambicensis*, *Dactyloctenium australe* and *Sporobolus nitens*. These grazing lawns are important because they support high numbers and a high diversity of herbivore species.

Experimental design

In 2000 we created an experimental mosaic of short grass patches in open savanna woodland, dominated by the tall grasses *Eragrostis curvula* (Schrad.) Nees, *Panicum maximum* Jacq. and *Sporobolus pyramidalis* with bush encroachment of *Dichrostachys cinerea* (L.) Wight & Arn., *Acacia spp* and *Gymnosporia senegalensis* Loes.. Subsequently, we maintained the short patches with a lawn mower at a height of around 5 cm, in contrast with the surrounding tall grass matrix of around 25 cm. The experimental mosaic consisted of short grass patches of different size and with varying nutrient input. In a basic layout of adjacent 8x8 m treatment plots, short grass patches were created with a size of 1x1,

2x2, 4x4 and 8x8 meter (Fig. 2). We created 9 1x1 m, 4 2x2 m, 2 4x4 m and 1 8x8 m subplots per treatment plot to simulate disturbances at different scales. We applied slow-release NPK-fertilizer four times a year to half of the mown plots to create differences in nutrient input rate between patches. To patches of all sizes we applied 12 gram N, 3.9 gram P, 19.8 gram K, 22.1 gram Ca and 18.8 gram S per m² of short grass per year. Each combination of patch size and fertilization was replicated 4 times. This resulted in 32 8x8 m treatment plots (Fig. 2). Surrounding the 32 treatment plots we created 8 control plots of 1x1 meter. These control plots were covered by a cage of chicken mesh to exclude all mammalian herbivores. Half of these plots were fertilized. The control plots were mown and fertilized at the same time and in the same way as the 32 treatment plots. Because the control plots were protected from grazing we will refer to them as mown ungrazed plots, compared with the mown grazed (treatment) plots and the unmown but potentially grazed matrix vegetation. The mowing treatment was applied during one year. The fertilization treatment was applied for around two years. We measured vegetation characteristics to study how patch size and fertilization treatment affected the grazing – vegetation feedback after we stopped the initial mowing disturbance.

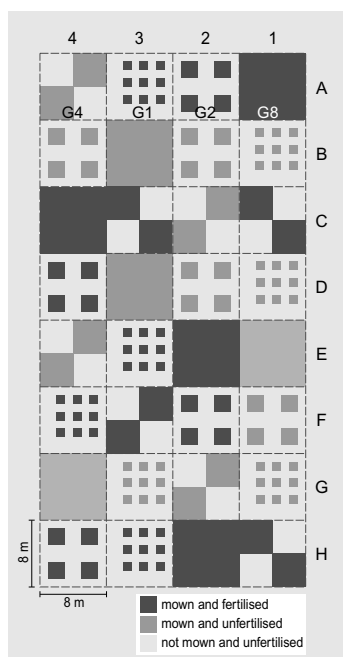


Figure 2 - The experimental layout, existing of 8 x 8 meter treatment plots with a combination of two treatments (patch size and fertilizer application). Manipulated patches are shown in black and grey; the shaded background represents the untreated matrix of tall grass and shrubs. Half of the plots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

Vegetation characterization

Once a month we measured the height of the vegetation with a round disc of 46 cm width and a weight of approximately 460 grams. The disc, with a hole in the middle, was dropped along a pole with a height scale in cm. The height was measured to the nearest cm at 1 point in the middle of the 1x1 m (also in the control plots) and 2x2 m subplots. In the 4x4 m and 8x8 m subplots the vegetation height was measured in a grid of points 1 m apart and 1 m from the edge of the patch, resulting in 9 and 49 points for the two treatments respectively.

We determined the species composition of all the treatment plots January 2001 and July 2004 within 2 by 2 meter quadrates in the middle of each plot. We identified all grass species and estimated their percentage projected cover visually using the Londo scale (Londo 1976). For the 4x4 m and 2x2 m treatment plots, the quadrate was placed in the same subplot for both years. For the 1x1 m treatment plots, 4 subplots were selected (the same ones for both years) to get a total survey area of 2 by 2 meter. We identified species and estimated their cover for each of the 4 subplots and averaged the 4 cover estimates per species before further analysis. Using the same method, we also measured the species composition in the control plots and in the matrix. For the matrix we measured the species composition in the 2x2 m matrix subplots in A4, C1, F3 and G2 (see Fig. 2), where the same subplots were measured in both years.

Animal visitation

We directly observed the visitation of different grazer species to the different treatments. The experimental site was situated on a hill slope. From the opposite hillside (about 450 meters from the experiment) there was an open view on the experimental site. From October 2000 up to November 2002, we observed for a total of 903 hours during separate 3 hour observation periods. For each observation every minute the position of the animal was recorded (according to the grid of 8x8 m cells shown in figure 2) together with the species and its behavior. Behavior was separated in two classes: grazing and other. For a full description of the methods see chapter 5.

Soil parameters

We took soil samples in the treatment plots as well as in the surrounding matrix in November 2004 to test if there were any long-term treatment effects on the soil. Per treatment plot 5 samples were taken randomly distributed over the mown subplots and 5 were taken randomly distributed in the surrounding matrix of each treatment plot. Samples were taken with a 5 cm diameter soil core from the upper 10 cm of the soil and dried at 105 °C. The 5 samples were pooled and 1 mixed sample was taken to the lab for the treatment plots and matrix separately, resulting in 64 samples. We ground the samples and analyzed them for total C and total N (using the Dumas dry combustion method), texture in three fractions (clay, silt and sand), electric conductivity (EC), pH (using a KCL solution) and extractable concentrations of Na, Ca, Mg and K. For a detailed description of the used methods see Manson and Roberts (2000).

Data analysis

Vegetation development

We first aggregated the vegetation height data as the average of the pseudo replicates per 8x8m treatment plot per measuring date. These averages were again aggregated as the average per treatment plot per season per year, dividing a year in 4 seasons; late wet (lw, January to March), early dry (ed, April to June), late dry (ld, July to September) and early wet (ew, October to December). These season classes were based on long-term rainfall data that are available for HiP. First of all, we wanted to know how the height in the ungrazed, control plots developed relative to the grazed plots. These ungrazed plots only had one size (1x1 m) and we, therefore, excluded patch size in this analysis. We tested for a difference between the ungrazed and grazed plots with a univariate analysis of variance with the factor grazing and fertilization. Time (season periods numbered chronologically) was included as a covariate in this model to account for the fact that height showed a long-term increase over the course of the experiment. Subsequently, we excluded the ungrazed plots to test how patch size and fertilization affected vegetation height in our grazed experimental plots with a univariate analysis of variance with fertilization and patch size as factors. Again we included season as a covariate in the model. After the identification we divided the grass species in two functional types; stoloniferous, lawn-forming species ('lawn grasses') and species with a caespitose growth form ('bunch grasses'). Three lawn-forming species were observed in the experiment; *Digitaria longiflora*, *Dactyloctenium australe* and *Sporobolus nitens*. For each treatment plot and for the matrix and control plots we summed the % cover of all lawn species into a percentage lawn cover for each plot. Using a univariate analysis of variance, we tested the effect of year, fertilization and size (as fixed factors) on the total cover of lawn grasses. In this analysis we included the matrix and control plots as a level in the fixed factor patch size.

Total grazing pressure

Before further analysis we aggregated the total number of observed grazing minutes as the sum of observed grazing minutes over all herbivore species per 8x8m treatment plot. A detailed analysis per species is presented in chapter 5. We calculated grazing pressure per square meter by dividing the aggregated sum of grazing minutes per plot by the total area of short grass in a plot (9, 16, 32 or 64 m²). Finally we calculated an average observed grazing pressure per week by dividing the minutes per square meter per plot by the total of 903 observation hours and multiplying these values with 168 hours in a week. We tested whether a possible generic effect of patch size (1, 4, 16 or 64 m²) on grazing pressure depended on fertilization using a univariate analysis of variance with the logarithm of patch size as a covariate and fertilization as a fixed factor. The log of patch size was used to make the distance between patch sizes equal and allow a linear regression between grazing pressure and log (size).

Soil parameters

We tested for an effect of treatments on all soil parameters using a univariate analysis of variance with the fixed factors, patch size and fertilization. To test whether soil parameter values differed between matrix and experimental plots we divided the data in three groups; matrix, unfertilized mown plots, fertilized mown plots. Using a one-way analysis of variance followed by Student-Newman-Keuls *a posteriori* contrasts we tested for differences between these groups.

Results

Vegetation development

The temporal dynamics in vegetation height depended on the presence of grazers. Vegetation height increased more in the ungrazed plots than in the grazed plots (Fig. 3, interaction grazing \times time, $F_{1,554} = 65.795$, $P < 0.01$). Vegetation height increased faster in the unfertilized plots than in the fertilized plots (interaction fertilization \times time, $F_{1,435} = 14.155$, $P < 0.01$). Furthermore height increased more in the 1x1 m patches than in the larger patch sizes (interaction size \times time, $F_{3,435} = 3.837$, $P = 0.01$). The effect of patch size also depended on fertilization (interaction fertilization \times size, $F_{3,435} = 8.329$, $P < 0.01$, Fig. 4 shows Student-Newman-Keuls *a posteriori* results). We included log (patch size) as a covariate in the analysis of variance model, with fertilization as a fixed factor, to test the generic effect of patch size that can be seen in figure 4. Vegetation height decreased with increasing patch size in the fertilized plots, while the height was constant for the different sizes in the unfertilized plots (interaction fertilization \times log (size), $F_{2,445} = 12.856$, $P < 0.01$).

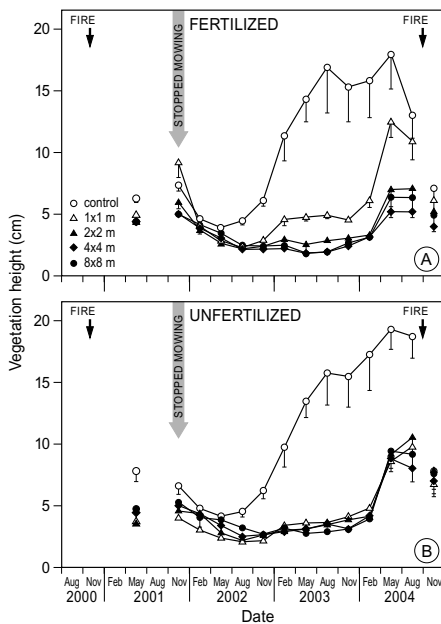


Figure 3 - Mean vegetation height (-1 s.e.) over time for fertilized (A) and unfertilized (B) plots and different levels of size of short grass patches, including control plots that were protected from grazing. Height data is aggregated as the average per treatment per season per year, according to the seasons that are explained in the methods section. The experiment was burnt just after it was created, half a year before we started height measurements and once again at the end of the experiment before our final height measurement.

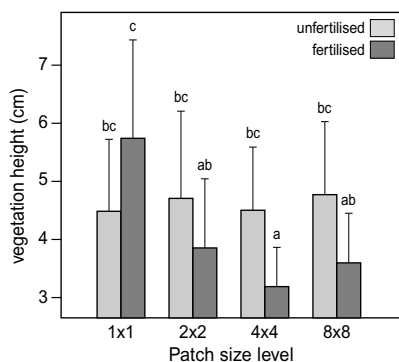


Figure 4 - Mean vegetation height (+ 1 s.e.) for different levels of size of short grass patches (see fig. 2) and fertilizer application. Different letters indicate a significant difference between treatments ($P < 0.05$, Student-Newman-Keuls test after two-way analysis of variance).

The effect of patch size on cover of lawn grasses depended on the year (Fig. 5, interaction size \times year, $F_{5, 66} = 7.354$, $P < 0.01$). In 2001 there was no difference in the cover of lawn grass between the different patch sizes (including the matrix and control) and the cover was close to 0 for all these treatments (Fig. 5A). In 2004 the cover of lawn grasses had increased in the 8x8 m plots with respect to the other patch sizes (including the matrix and control) (Fig. 5B). The effect of patch size on cover of lawn grass also seemed to depend on fertilization, but this interaction was not significant (interaction fertilization \times size, $F_{4, 66} = 2.197$, $P = 0.079$, also see Fig. 5B). For the 2004 data we therefore included log (patch size) as a covariate in the analysis of variance model to test if the generic effect of patch size depended on

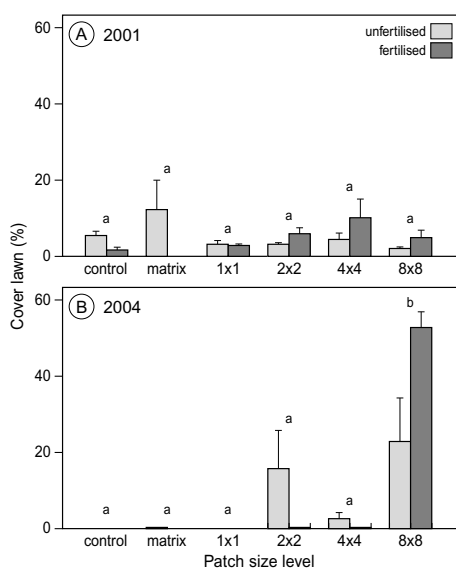


Figure 5 - Mean percentage cover (+ 1 s.e.) of lawn grass species in the control plots, the matrix vegetation and the different levels of size of short grass patches and fertilizer application. In the matrix vegetation we did not have fertilized plots. The results are shown for 2001 (A) and 2004 (B). Different letters indicate a significant difference between treatments ($P < 0.05$, Student-Newman-Keuls test after two-way analysis of variance).

fertilization. In 2004 the increase in lawn cover was indeed larger in the fertilized plots than in the unfertilized plots (interaction fertilization \times log (size), $F_{2, 29} = 6.898$, $P = 0.004$).

Total grazing pressure

The following herbivore species were observed grazing in the short subplots (within brackets the number of grazing minutes for the species as a % of total observed grazing minutes); warthog (*Phacochoerus aethiopicus*, 50%), impala (*Aepyceros melampus*, 33%), zebra (*Equus burchelli*, 12.3%), white Rhino (*Ceratotherium simum*, 1.9%), nyala (*Tragelaphus angasi*, 1.9%), wildebeest (*Connochaetes taurinus*, 0.4%), buffalo (*Syncerus caffer*, 0.3%) and waterbuck (*Kobus ellipsiprymnus*, 0.2%). Total grazing pressure of all species together increased with patch size in the fertilized plots in contrast with the unfertilized plots where it remained constant (Fig. 6, interaction fertilization \times log (size); $F_{2, 29} = 18.665$, $P < 0.01$, log (size) as covariate).

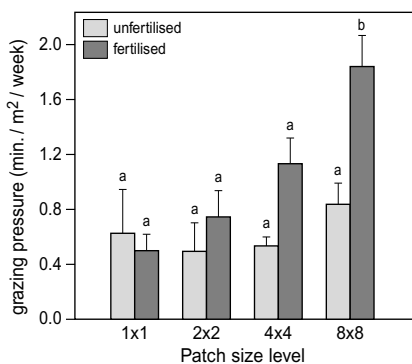


Figure 6 - Grazing pressure (+ 1 s.e.) for different levels of size of short grass patches (see fig. 2) and fertilizer application. Different letters indicate a significant difference between treatments ($P < 0.05$, Student-Newman-Keuls test after two-way analysis of variance).

Soil parameters

The fertilized plots had a higher electrical conductivity (EC) than the unfertilized plots ($F_{1, 24} = 8.395$, $P = 0.008$), as well as higher concentration of extractable Ca ($F_{1, 24} = 8.585$, $P < 0.01$), Mg ($F_{1, 24} = 5.463$, $P = 0.028$) and K ($F_{1, 24} = 25.542$, $P < 0.01$). The pH was significantly lower in the fertilized plots than in the unfertilized plots ($F_{1, 24} = 5.177$, $P = 0.032$). The soil of the matrix vegetation did not differ from the mown unfertilized plots ($P > 0.05$), except for the potassium concentration. The soil concentration of K was higher in the matrix than in the unfertilized mown plots, but lower than in the fertilized mown plots ($F_{2, 61} = 12.377$, $P < 0.01$). Total C and N content of the soil, soil texture and soil sodium concentration were not significantly different between any of the size and fertilization treatments ($P > 0.05$).

Discussion

The results showed that in our study site enhanced nutrient availability induced the formation of grazing lawns, but only above a certain threshold disturbance resolution. After we stopped mowing the vegetation height started increasing, but the strength of this increase depended on whether the plots were grazed and on the resolution and nutrient status of the plots. The height increased faster in the unfertilized plots with finer resolution. Grazing seemed to keep grass short at grazing lawn level in the coarser, fertilized plots (4x4 and 8x8 m). Two and a half years after we had stopped mowing a shift in grass community composition had taken place in the least-fragmented fertilized plots, showing a strong increase in the cover of lawn species. Overall grazing pressure was also significantly higher in those plots. In conclusion, as hypothesized, our results suggest that the positive feedback between grazing and grazing lawn formation depends on nutrient status as well as the resolution of the initial disturbance.

We showed that colonization of stoloniferous lawn grass species was most clear in the fertilized 8x8 m plots (Fig. 5B), where grazing pressure increased most strongly (Fig. 6). This result supports the idea that lawn grasses can colonize under circumstances of high nutrient availability in combination with a high grazing pressure because these grasses show compensatory growth in response to grazing in contrast with the grazing sensitive bunch species (McNaughton 1983b; Augustine and McNaughton 1998). The evolution of grazing tolerance in grass species is still under debate. It has been attributed to convergent selection processes to cope with drought, which results in traits that also make plants more tolerant to grazing, e.g. basal meristems and short growth-form (Milchunas et al. 1988; Augustine and McNaughton 1998). In this respect it is interesting to note that many lawn-forming grasses in Africa are halophytes (i.e., adapted to physiological drought due to high salinity) and occur in semi-dry to dry areas.

Our results suggest the existence of two types of lawns; patches of potentially tall bunch grass that are temporarily kept short (temporal lawns) and patches of short, stoloniferous grazing tolerant lawn grass species (long-term lawns). Field examples of temporal lawns are patches of *Themeda triandra* that are grazed and kept short for some time period by buffalo and white rhino in Hluhluwe-iMfolozi Game Reserve (Owen-Smith 1988 and personal observation). Our results show that bunch grass patches that are grazed short can remain in a temporal lawn state for a considerable period (Fig. 3A, 3 years) before a community shift takes place to a compositional lawn. Archibald and Bond (2003) argued that a grazed patch needs to stay short for >4 years to be colonized by stoloniferous lawn grasses. Our results indicate that this process can be somewhat faster, because lawns had formed within 4 years after we created the short grass patches. Moreover, this community shift seems to depend on scale of the disturbance and only occurs in the coarser grain patches whereas in the finer grained 4x4 and 2x2 patches the vegetation remains in a structural lawn state. We hypothesize that the

temporal lawns are less stable than the long-term lawns, because the bunch growth form will directly grow back to a tall state again if grazing pressure decreases or e.g. rainfall increases while stoloniferous species will remain short for a considerable period even when grazing pressure decreases. The latter is in fact observed in enclosure experiments (H. Olff and W.J. Bond, personal observations). In this respect, Archibald and Bond (2003) developed an interesting theory on the effect of fire frequency on the persistence of grazed patches and the community shift to long-term grazing lawns. They hypothesize that frequent fires create a more homogenous grazing pressure; hereby decreasing the pressure on grazed patches and preventing formation of long-term grazing lawns (see also Archibald et al. 2005).

The main driver behind lawn formation in our study was grazing in interaction with increased soil fertility. In the east African savanna systems short grasslands support dense herds of medium-sized grazers such as wildebeest, zebra and gazelles (McNaughton 1984). Owen-Smith (1988), however, suggested that only the megagrazers, white rhino and hippo, can create real permanent grazing lawns. He acknowledges that dense herds of e.g. wildebeest in the Serengeti transform tall grasslands into short grass but argues that their intense grazing is too temporal to induce changes in grassland composition. In our study warthog were responsible for 50% of the grazing pressure (number of observed grazing minutes) and impala 33%. In the fertilized 8x8 plots, where grazing lawns developed, warthog were responsible for 65% of the observed time grazed and impala for 26%, while white rhino only contributed 1.5%. I.e. in our study warthog and impala seemed to be mainly responsible for maintaining structural lawns and promoting the colonization of stoloniferous lawn grasses. So the fact that white rhino is considered to be the main driver behind creating grazing lawns in Southern Africa savannas (Owen-Smith 1988), might very well underestimate the role of the smaller grazers, like warthog. Rather, we propose that a diverse community of large and small herbivores promotes lawn formation, where megaherbivores are responsible for the first disturbance but smaller species (help) keep the grass short and promote colonization of stoloniferous grazing lawn species.

We choose two contrasting disturbance types to illustrate our hypothesis (Fig. 1). In reality there are many more disturbance types that could possibly replace or complement our examples. Large termite mounds, for example, could play the same role as middens or wallows. In fact, studies indicated the role of these large mounds as grazing hotspots (Holdo and McDowell 2004, Mobaek et al. 2005). More studies are needed that quantify these small-scale disturbances in savanna grasslands to get better insight in the processes that drive grazing lawn formation. Our results suggest that the spatial resolution of the disturbance is an important characteristic that should be measured.

In conclusion, our results suggest that scale-dependent foraging decisions influence formation of local lawn-bunch mosaics. On other spatial scales other factors can determine lawn grass distribution. Therefore it is important to see our

results as part of a nested design of mechanisms that create lawn-bunch patterns, where our study gives insight in within-grassland pattern formation. On landscape scales the catena position, distance to water and variation in soil type have been argued to influence lawn formation (Bell 1971; Swemmer 1998). On an even higher regional scale potential occurrence of grazing lawns is probably determined by parent material, rainfall, herbivore geographic distributions, and possibly fire regimes (East 1984; Archibald et al. 2005).

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7

The impact of resource heterogeneity on large grazer resource partitioning at different spatial scales: a synthesis.

Joris P. G. M. Cromsigt

Emmanuel, you worked with us for just a short period of 9 months in 2004, but an important one! Thanks for sending me up in trees while walking long transects in the field. Walking these transects you were in your element, not when you had to hold a clipboard to write down species (though you did a good job with this too!) I hope you're enjoying your new job as a field ranger in Thanda Private Game Reserve...

Partitioning resources at different spatial scales

Research on partitioning of resources among savanna herbivores has a long history of empirical research, with a strong basis in east Africa. This work has resulted in a wealth of knowledge on differences in species diets and behaviors. However, the spatial dimension of resource partitioning has been underexposed in these studies, possibly because many studies were performed in systems without much small-scale heterogeneity, such as the Serengeti plains (Fryxell et al. 2005). Recently, theoretical work has included spatial aspects to explain resource partitioning among large herbivores (Du Toit and Owen-Smith 1989, Ritchie and Olff 1999, Owen-Smith 2004, Carbone et al. 2005, Fryxell et al. 2005). These studies discussed how spatial variation in resource quality allows different-sized species to distribute differently over the landscape and hence partition resources (Du Toit and Owen-Smith 1989, Owen-Smith 2004, Carbone et al. 2005), because of the allometry of resource quality requirement. The spatial scale of heterogeneity in these studies varied widely, from the habitat (Du Toit and Owen-Smith 1989) and home range level (Haskell et al. 2002, Carbone et al. 2005) to the role of large-scale landscape migrations (Fryxell et al. 2005). Moreover, Ritchie and Olff (1999) showed how differences among species in the scale at which they perceive their environment might lead to difference in resource use at the local patch scale. Concluding, these studies emphasize the importance of resource heterogeneity for species coexistence, but the spatial scale varies and is sometimes not even explicitly stated. Moreover, when I started this work, empirical work on large African herbivores including spatial aspects was still very limited. Therefore I choose to use a range of empirical methods (from purely observational to experimental) to investigate how spatial heterogeneity might affect the distribution and resource partitioning of large grazers at different spatial scales. In the previous chapters I have shown that the spatial dimension is indeed an important attribute to understand how large grazers partition their resources at different spatial scales.

In chapter 3 I showed that 6 common grazer species in Hluhluwe-iMfolozi Park (HiP) were differently distributed over the landscape. Smaller grazers occurred more spatially aggregated in the landscape than larger species that were more evenly distributed. However, small non-ruminant herbivores were surprisingly uniformly distributed, choosing a wider variety of habitats than similar-sized ruminants. I related these distributions to differences in habitat quality selectivity among species, specifically selection of habitat covered with grazing lawns of high-quality grasses. Impala, wildebeest and warthog preferred the areas with high cover of grazing lawns. Densities of the more uniformly distributed species were not (zebra and buffalo) or much less (white rhino) influenced by grazing lawn abundance. These different distributions of the grazers, which depended on resource quality distribution and preference, lead to a different use of the landscape, and seems to contribute to resource partitioning among the grazers on a landscape scale (5-50 km).

At a finer scale (1 – 10 km, chapter 4) I showed that grazer assemblages differed significantly among different grassland types, especially among bunch and lawn grass dominated sites. The overall grazer visitation on the lawn dominated sites remained high throughout the year, only dropping after prolonged periods of drought, but was never lower than the visitation to the bunch grassland. The sites dominated by lawn-forming grasses were visited by twice as many species per day as the bunch grassland and overall visitation rate (number of individuals per day) by grazers was much higher on the lawn-dominated sites. These lawn-dominated sites were visited by herbivores of all size, while the bunch grassland was dominated by larger species, white rhino and especially buffalo. Fire temporarily affected the grazer species composition of the bunch grassland. It has been suggested to be an important factor that rearranges the spatial distribution of herbivores (Coppock and Detling 1986, Moe et al. 1990, Wilsey 1996, Tomor and Owen-Smith 2002, Archibald and Bond 2004, Archibald et al. 2005), because it increases resource availability in grasslands that are of generally poor quality (Van de Vijver 1999). In Chapter 4 I showed that fires increased visitation of intermediate to large sized grazers to the bunch grassland but only for a short period of time. Moreover, in post-burn periods total grazer visitation approached the level of visitation in the lawn grasslands but did not exceed it. Fire clearly did not influence all grazer species equally and may be especially important for larger species, such as buffalo, zebra and wildebeest, and at certain points in time such as after long dry periods. Brooks and Berry (1980) showed that smaller grazers in HiP responded less strongly to burns than larger species based on a large dataset from transects that were distributed all over the park and attributed this to the relatively small home ranges of small grazers. Concluding, results suggested that large grazers species differ in their use of different grassland types, which might contribute to their coexistence. The bunch grassland was mainly used by buffalo and white rhino, and by zebra and wildebeest for a short period after a fire. Small grazers, impala and warthog, did not visit this grassland type. The lawn-dominated sites were visited by all species (though the extent of visitation strongly differed among species). Moreover, I found no clear temporal partitioning among species on these lawns, the visitation of all species increased and decreased at the same time. This contrasts the situation in the Serengeti, where a grazing succession has been suggested with larger species facilitating grass height for the smaller grazers (Vesey-Fitzgerald 1960, Bell 1971). Grazing lawns in HiP seem to provide a resource hotspot to all species, possibly because of the high availability of essential elements, such as sodium and phosphorus. The fact that the use of these lawns is not clearly temporally partitioned among species indicates that these species partition their resources at other sites or at an even finer scale responding to within grassland variation. This would especially apply to the small grazers, since the larger grazers seem to combine visitation to the lawns with visitation to the bunch grassland.

At an even finer scale, the within-grassland patch level (1-100 m), I showed that the way short grass patches are distributed within a grassland (at fine or coarse

resolution) influenced the grazing intensity of different grazer species (chapter 5). The smaller species, impala and especially warthog, preferred the larger, more homogeneously distributed short grass patches, while the larger species, zebra and white rhino, had no clear preference for resource grain. These results supported the prediction of Ritchie and Olff (1999) that species differ in the scale of resolution at which they sample their resource environment. They, moreover, showed how this difference in sampling detail can contribute to the coexistence of these grazers. However, I did not find evidence for their prediction that body size determines the patch size in which a species will exclusively use resources. In this, it is important to realize that our largest patch size was 64 m², much smaller than the several ha size grassland patch discussed in chapter 4. This might explain why a short grass specialist such as wildebeest hardly visited the experiment. It is important to repeat the experiment with larger patch sizes. I expect that in such an experiment the large plots, such as the 1 ha plot in chapter 4, will be visited by all species, but that the smaller plots are dominated by the smaller species.

Resource heterogeneity as a complex landscape

The previously discussed results make clear that species do not simply partition resources at one spatial scale. The question is what factors determine the distribution of resources at these scales. To understand resource partitioning and ultimately species coexistence we need models where spatial scale is an integral trait of the mechanisms that explain distribution of the resources. Models that integrate ecological process and spatial scale have been developed in landscape ecology (Wu and Loucks 1995) and have been applied to understand tree-grass patterns in savanna systems (Coughenour 1991, Coughenour and Ellis 1993, Gillson

2004). According to such models the resource landscape that grazers face and have to partition can be seen as a complex system where a hierarchy of different factors influences the heterogeneity of resources and different factors influence resource heterogeneity at different spatial scales. In this thesis I mainly defined resource heterogeneity as variation in short (lawn) and tall (bunch) grass patches at different spatial scales. In the following paragraphs I will illustrate the hierarchy of factors that determines the complex resource landscape that savanna grazers can partition.

Determinants of resource heterogeneity at the landscape scale

The general geological structure of HiP goes back to intense fracturing and faulting due to the attempted Gondwana breakup (180 million years ago) and final drifting (140 million years ago) (Conway et al. 2001). Due to the volcanic activity during this period lava flows built up a mountainous landscape in a previously fairly level area culminating into the Drakensberg in the east of Kwazulu-Natal. Since this period the landscape eroded from the Drakensberg eastwards towards

the sea. A tilt of the African continent about 120 million years ago, and again one million years ago, of about 1 degree eastward caused a second uprising and is mainly responsible for the currently visible large-scale topographic patterns

in HiP (King 1970, Conway et al. 2001, Fig. 1C). The tilt caused a strong increase in relief towards the west with a development of steep slopes and the rivers to be steepened towards the east. Since then the river valleys have broadened and eroded the uplifted country, resulting in broad, fairly level, valleys (Fig. 1C). This topography influences the resource heterogeneity in HiP at a landscape scale. Large-scale altitudinal variation significantly explains variation in grazing lawn cover (Fig. 1, 2A, Pearson $r = -0.32$, $P < 0.01$). Mean annual rainfall is closely correlated with altitude (Pearson $r = 0.62$, $P < 0.01$, Fig. 2B) and similarly explains variation in proportion of grazing lawn (Pearson $r = -0.31$, $P < 0.01$, Fig. 2C). Concluding, grazing lawns are limited to the lower, relatively dry parts of HiP. This pattern of grazing lawns that prevail in the dryer parts of HiP might emerge from the traits of individual lawn plants. The traits that make grasses tolerant to grazing also increase the drought resistance of these plants and *vice versa* (Coughenour 1985). The feedback mechanisms between plants and grazers that induce grazing lawn formation (chapter 6) might be strongest under dry conditions, where drought acts as a convergent selection pressure (Milchunas et al. 1988). The fact that semiarid grasslands are often dominated by short, stoloniferous grasses supports this proposition. However, while high rainfall seems to limit grazing lawn distribution at high altitudes, other factors are clearly also important in determining grazing lawn distribution in the range of 100 – 300 meters (Fig. 2A). To understand this pattern we have to look what factors create lawn – bunch grassland patterns at finer, regional scales.

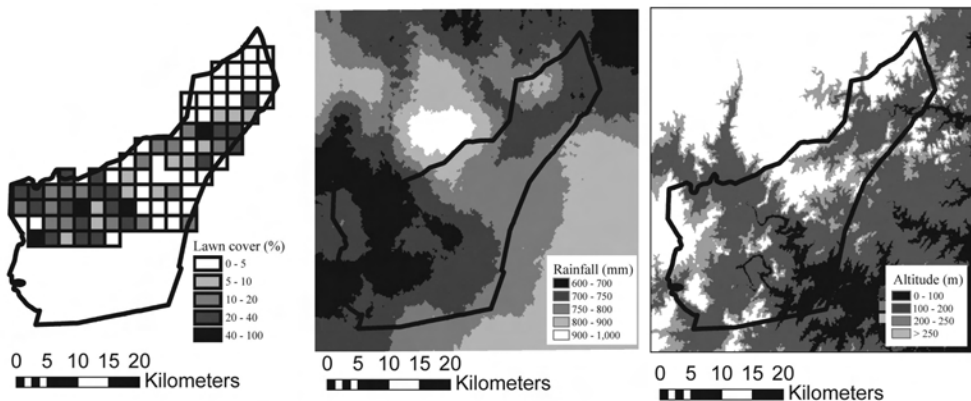


Figure 1 - Proportion of grazing lawn per 2.5 by 2.5 km grid cell in Hluhluwe-iMfolozi Park, based on line transects that cross these grid cells as described in chapter 3 (A). Furthermore, the figure shows average yearly rainfall (B) and altitude (C) in HiP. The rainfall data for Hluhluwe-iMfolozi Park originates from Schulze (1997), and represents a long-term annual average.

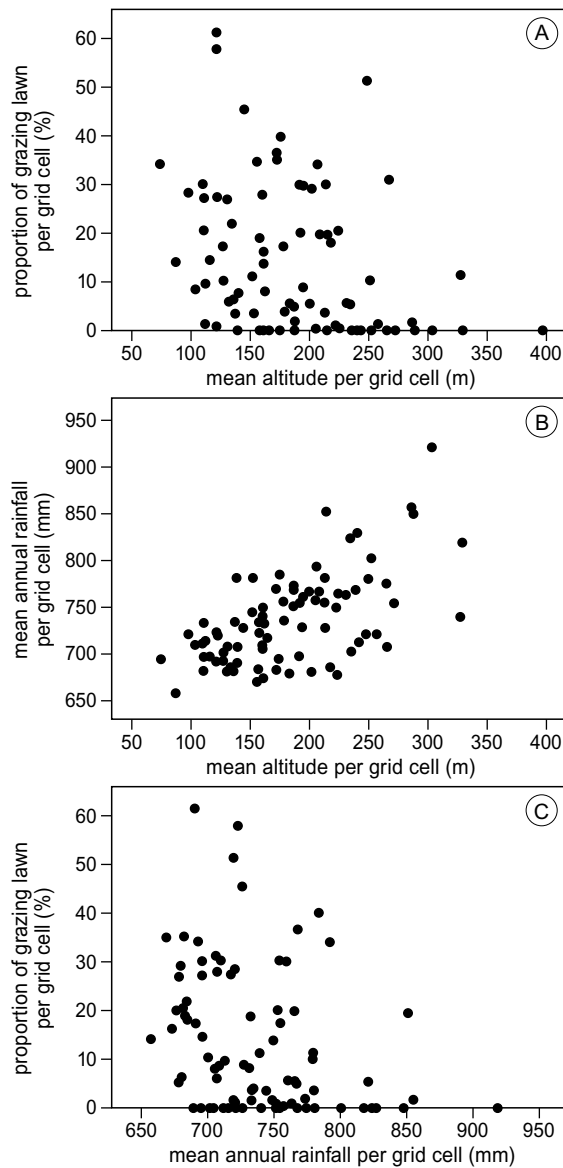


Figure 2 - Scatter plots for the proportion of grazing lawn per 2.5 by 2.5 km grid cell (as shown in Fig. 1) versus the average altitude (A), average altitude versus average rainfall per grid cell (B) and the proportion of grazing lawn versus average rainfall (C) per grid cell.

Determinants of resource heterogeneity at a regional scale

Regional variation in soil characteristics, such as soil texture, organic matter content and slope, influences water availability and should, therefore, influence regional grazing lawn distribution patterns. In HiP lawn cover decreased with increasing soil clay content and was close to absent on soils with clay content higher than 40% (Pearson $r = -0.52$, $P < 0.01$, Fig. 3A). Clay content was not significantly correlated with elevation in this altitudinal range ($r = 0.10$, $P = 0.54$) and altitude itself did not significantly explain variation in lawn abundance ($r = 0.26$, $P = 0.11$). Next to clay content, lawn cover increased with increasing soil salinity ($r = 0.53$, $P < 0.01$, Fig. 3B), measured as the electrical conductivity of the soil (Manson and Roberts 2000). Salinity was not significantly correlated with the clay content of the soil ($r = 0.14$, $P = 0.52$), so salinity and texture might independently influence lawn-bunch distribution. In east Africa many of the short grass species seem to be halophytes, growing in saline areas, such as sodic sites (Hamilton et al. 2001, H. Olff, personal comments). Moreover, Semple et al. (2003) showed that from 30 different grass species, only the stoloniferous species performed well on saline sites. So, next to water stress, lawn species might be better able to cope with the physiological stress that results from the salty environment than caespitose species. This is supported by the fact that response to salt and drought stress in plants has been attributed to comparable biochemical-molecular mechanisms and possibly even originates from the same genes (Wang et al. 2003). Moreover, intense grazing leads to an increase in the proportion of bare soil, which leads to increased soil evaporation and consequently decreased soil water content as well as increased salt concentration. Concluding, grazing, drought and salinity

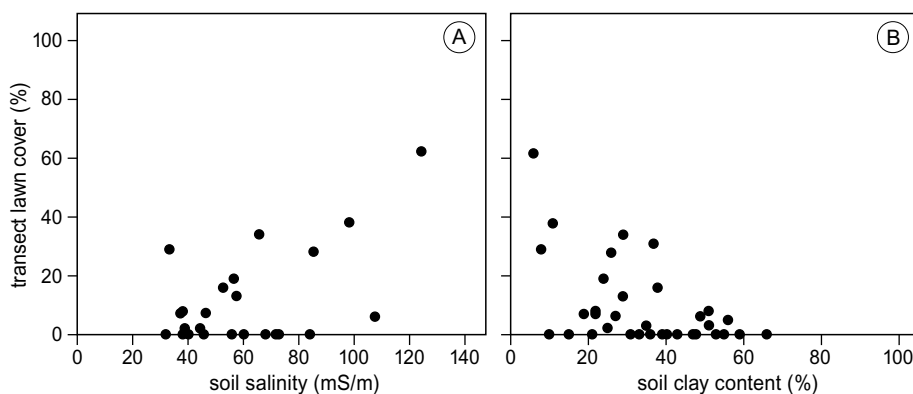


Figure 3 - Dots show the average grazing lawn cover that we measured on 39 transects of 100 meter long in the northern half of the park, all in the altitude range of 100-300 meters (lawn cover was determined as the percentage of three dominant grass species, measured every 10 meters on the transect, that was a grazing lawn species). Grazing lawn cover is plotted against soil clay content (A) and soil salinity (B), both determined from a pooled sample of 10 subsamples evenly distributed over each transect. Salinity was measured as electrical conductivity and clay content as the percentage of particles < 0.002 mm (Manson and Roberts 2000).

might act as converging selection pressures that promote stoloniferous lawn species above bunch grass species. Unfortunately, there are hardly any studies that investigated the relative effect of these pressures on stoloniferous species, making the exact mechanisms that cause grazing lawn development unclear.

Though the exact mechanisms have to be further tested, regional variation in soil type creates variation in grassland types, and consequently resource availability at regional scales. However, as figure 3 nicely illustrates, next to soil texture and salinity other factors determine the relative abundance of lawn versus bunch grass types. Even where texture and salinity seems to be optimal, lawn abundance can still be low. In other words why do lawns form on some sandy soils but not on others? I suggest that mechanisms at a local scale, where herbivores and resources interact, explain why lawns emerge on some soils and not on others (chapter 6).

Determinants of resource heterogeneity at a local patch scale

Based on experimental results I showed that local herbivore-resource interaction depended on the nutrient state and spatial grain of resource patches (chapter 5 and 6). The experiment in which this was shown, was situated at an altitude of 150 meters with a soil clay content of around 14 %. But while soil texture and altitude were suitable for grazing lawn formation (Fig. 2, 3) lawns only formed after a long-term coarse-scale disturbance of the bunch grass in combination with an increased nutrient input. I hypothesized that this combination of increased nutrient input and coarse scale disturbances of bunch grass that was simulated is naturally represented by features of megaherbivore habitats, such as game paths, wallows and middens. As Owen-Smith (1988, 2004) suggested, megaherbivores play a crucial role in creating and maintaining grassland heterogeneity. But while he emphasized their grazing impact, I suggest that they disturb, open up and fertilize the bunch vegetation (in features such as middens or wallows, chapter 6) which consequently attracts other grazers. The combined grazing pressure of large and small grazers then induces lawn formation. This idea supports the hypothesis that diverse herbivore communities facilitate grassland heterogeneity (Du Toit and Cumming 1999, Fuhlendorf and Engle 2001). The previously hypothesized soil salinity tolerance of grazing lawn species might also play a central role in this grazer-resource feedback. By urinating and defecating at their disturbed places (middens/wallows) megaherbivores potentially increase the salinity of the soil, creating a competitive advantage for grazing lawn species over other grass species. As the lawn develops the proportion of bare soil increases, resulting in a further increase in salinity because of increased soil evaporation. Increased salinity increases the competitive advantage of lawn species etc. This role of soil salinity offers an alternative or additional mechanism next to the importance of increased N input in urine and dung patches, as proposed by Ruess and McNaughton (1984).

Concluding, in the previous paragraphs I showed how resource distribution can be defined as patches at different scales, where different processes determine the distribution of resources at these scales, changing from geological processes at

the largest scale, to biotic interactions at the smallest scale (Figure 4). I believe such conceptualization of spatial scale is essential to start understanding how large herbivores potentially partition resources across these spatial scales.

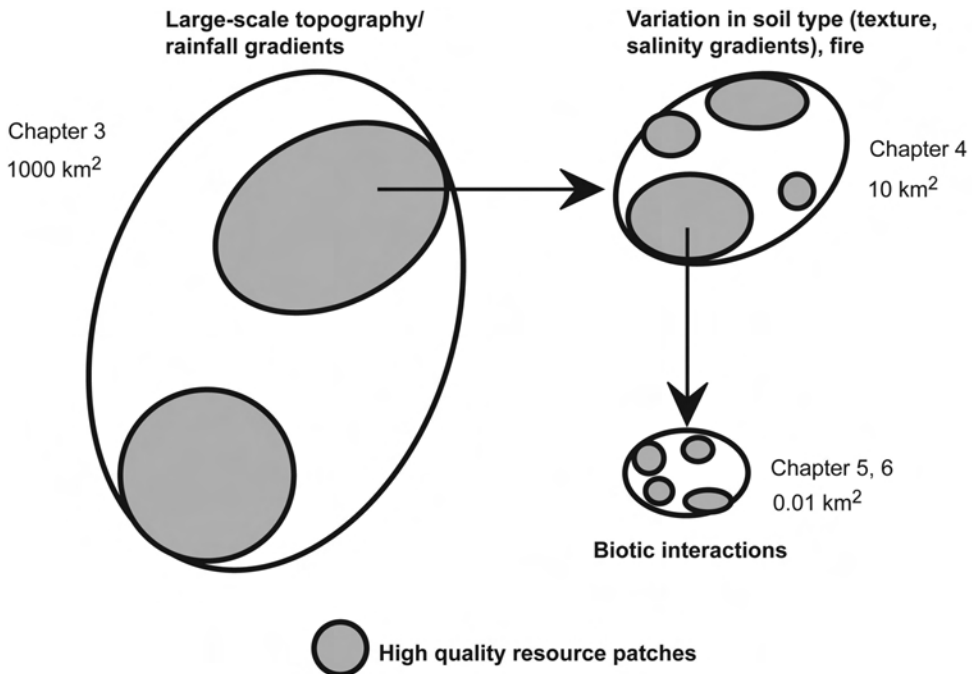


Figure 4 - A conceptual model of the resource distribution in Hluhluwe-iMfolozi Park. Patches of relatively high resource quality (high abundance of grazing lawn grasses) can be defined at different scales. Different processes mediate resource distribution at different scales and these processes are nested in a hierarchical design where large-scale processes impose constraints on finer scale resource distribution. Mechanisms at the finest scale, however, are responsible for emerging resource distribution patterns at larger scales. Note that this is a very simplified conceptual model, which should be elaborated for a wider range of resources (optimal and suboptimal), depending on species.

Resource heterogeneity and herbivore abundance

So far I have focused on spatial distribution and resource partitioning patterns of large grazers. I did not concretely discuss the impact of resource heterogeneity on actual population abundance. The densities of the 6 grazer species in HiP are high compared with other well-studied African savanna systems, with the total grazer biomass density close to that of Serengeti and much higher than Kruger NP (Fig. 5A). We have to take into account that the Serengeti is a very different system, where the grazer biomass density is dominated by migratory wildebeest (Fig. 5B). So large parts of the year biomass density is actually much lower in areas when wildebeest are absent. Brooks (1982) illustrated that in HiP zebra, wildebeest and buffalo populations are sedentary. Using radio-tracking data, he showed that individuals from sub-populations areas (defined as areas with limited movement across its boundaries) of these species were able to reach any part of the area they occupied within hours. Moreover, rainfall did not seem to influence movement across the sub-population boundaries. In other words local year-round biomass density in HiP might be high compared with the Serengeti system as well.

So why is grazer biomass density so high in HiP relative to these other reserves? It is appealing to philosophize that the answer to this question lies in the high spatial resource heterogeneity in HiP. Recent modeling studies show that population numbers are more stable in systems where resource heterogeneity is high (Illius and O'connor 2000, Owen-Smith 2004). Central to these studies is the availability of optimal and suboptimal resources in a species habitat. The optimal resource enables population growth, whereas the suboptimal resource acts as a buffer against population crashes, because animals switch to this resource before the optimal resource becomes depleted. Fryxell et al. (2005) argued that protected areas have to be sufficiently large so that animals can migrate between these resources or have to be very heterogeneous (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 kilometers apart (chapter 4, and Fig. 6). This fine scale heterogeneity in grassland types might be responsible for maintaining the stable, high density populations of grazers in HiP.

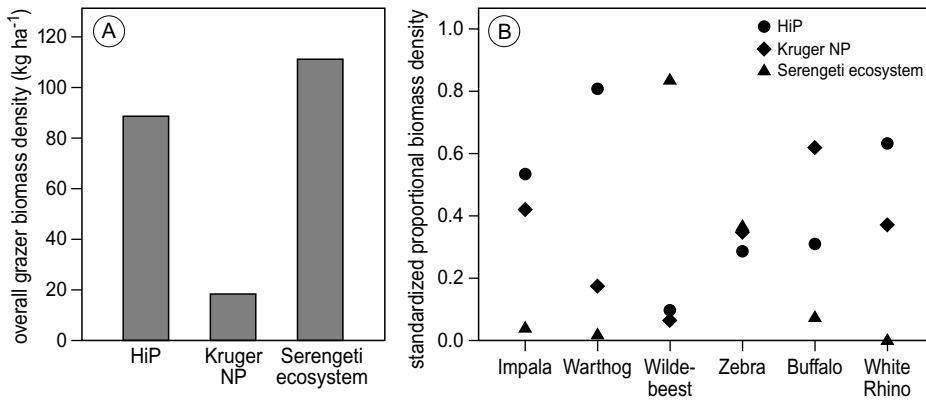


Figure 5 - Overall grazer biomass density (A, in kg per ha) for three different reserves, Hluhluwe-iMfolozi Park, Kruger National Park and the Serengeti ecosystem, and the standardized relative proportions of biomass density of the different grazer species (B) in these reserves. First of all relative proportions were calculated per species and per reserve and then these proportions were standardized per species to emphasize differences between reserves (species proportion for a reserve divided by the sum of proportions for this species over all reserves).

Resource heterogeneity and diversity

Can we translate these ideas from the effect of resource heterogeneity on population abundance of a single species to species diversity? After all, overall biomass density is not only high in HiP, but the park is also characterized by high relative densities of the smallest species (Fig. 5B). When translating heterogeneity to diversity it is important to assume that species differ in the scale of resource heterogeneity that they respond to (Ritchie and Olff 1999, Olff and Ritchie 2001, Owen-Smith 2004). In this thesis I present evidence at different spatial scales that support this assumption (chapter 3, 5). At the landscape scale smaller grazers, especially smaller ruminant grazers, were more spatially aggregated and responded more strongly to variation in habitat quality (chapter 3). At a much finer local patch scale results indicated the grain of resource patches influences grazing intensity of species differently (chapter 5). Smaller species might be more limited by the scale of resource heterogeneity than larger species that can travel larger distances (see also chapter 3). I, therefore, suggest that the scale of heterogeneity relative to the home range size of the smallest species is a crucial characteristic of savanna systems that influences herbivore diversity. This home range size for the smallest grazer in HiP, impala, is around 5-6 km² (Jarman 1970, Du Toit 1990). Although impala is mainly a grazer in HiP, the percentage of browse in their diet increases during the dry season (Botha and Stock 2005). From this thesis we know that impala highly prefers lawns above other grassland types (chapter 3, 4). If we assume that lawns represent the optimal resource for impala which they leave for tall grass and browse as suboptimal resource in the dry season, figure 6 shows that these optimal and suboptimal resources are amply available within an average

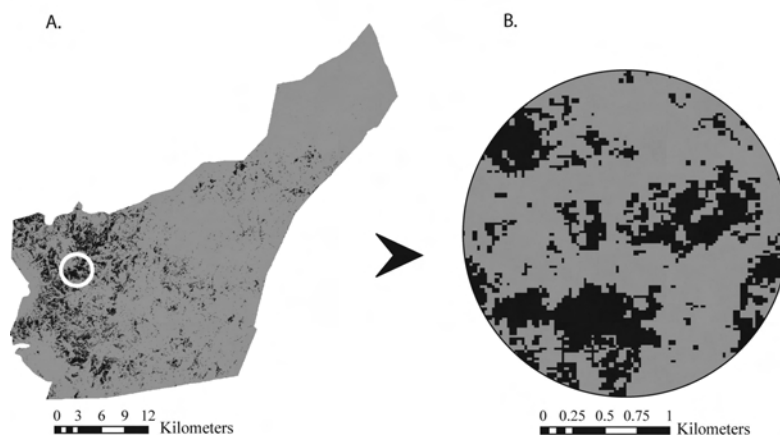


Figure 6 – A. Distribution of open grazing lawn areas (black areas) and other vegetation types, mainly dominated by caespitose grass species and shrubs (grey areas) in Hluhluwe-iMfolozi Park. This map is the result of an analysis of a 1995 LANDSAT-TM image (30 m² resolution) combined with ground-truthing of the different vegetation types (Meyer 1999). B. Zoomed in portion of the south-eastern part of the park (encircled in white in A), which represents more or less the size of an average impala home range in HiP.

impala home range, especially in the south-eastern part of the park. This might also explain why impala density is higher in this part of the park (chapter 3).

However, not only the smallest grazers have a relatively high density in HiP, but also the largest grazer by far, the White Rhino (Fig. 5B). Interestingly, this species has an unusually small home range size relative to its body size (in HiP 10-20 km², Owen-Smith 1988, while home ranges for wildebeest, zebra and buffalo are much larger (70-80 km²), Brooks 1982). Moreover, white rhino has been described as a species that responds to the same fine scale heterogeneity as the small grazers (Owen-Smith 1988, 2004). The fact that its very large size allows it to influence and create this heterogeneity might have allowed it to maintain small home ranges (chapter 6, Owen-Smith 1988). By creating this small-scale heterogeneity it not only facilitates itself but also the smaller grazers, as discussed earlier. The absence of white rhino from the Serengeti system and the low densities in Kruger NP compared with HiP might also explain why the densities of especially the smaller species are relatively low in these systems (Fig. 5B). The question remains why white rhino has such a small home range in contrast with the other large grazers. Possibly its mega size limits travel distance because its high food quantity requirement constrains time for non-foraging behavior (Owen-Smith 1988). Moreover, it has been suggested that a very large size might not be so advantageous and possibly even puts limits on digestive efficiency (Clauss et al. 2003, Clauss and Hummel 2005), for example because of a decreasing gut surface : gut volume ratio with body mass. In this respect the small home range of white rhino might be an

adaptation, resulting from the need to be sedentary to be able to maintain grazing lawns, keeping the grass in a highly digestible state (Owen-Smith 1988). In this way, this megaherbivore would compensate for its relatively low digestive efficiency by maintaining a high food quality.

Management of resource heterogeneity

In the previous paragraphs I already touched upon the theoretical continuum going from large reserves with coarse-grained heterogeneity to small reserves with fine-grained heterogeneity. Coarse-grained systems, where there are only large-scale gradients that affect resource quality and quantity, have to be sufficiently large for animals to find the right balance of optimal and suboptimal resources (as described by Fryxell et al. 2005 for the Serengeti). As explained above, model studies indicate that fine scale heterogeneity can counterbalance reserve extent, because optimal and suboptimal resources become available in home ranges of sedentary species. We need more empirical work to prove the existence of such a continuum. However, if it holds it would have wide implications for conservation planning. Focusing on reserve size would still be necessary in some cases (e.g. Serengeti system) but in places where the abiotic template is heterogeneous small reserves might be a good alternative. This offers new opportunities for areas where many different stakeholders compete for space, such as the province of Kwazulu-Natal where HiP is situated. In such areas the available scale of heterogeneity of e.g. topography or soil types should be an essential criterion for reserve planning.

Results from this thesis suggested that interacting mega and smaller herbivores promote resource heterogeneity at the local scale (chapter 6). This supports the suggestion that the diversity of herbivore communities is a significant aspect of savanna ecosystem functioning (Du Toit and Cumming 1999). Moreover, we emphasized the potential role of small herbivores in creating and maintaining heterogeneity in savannas (see also Prins and Van der Jeugd 1993). These results support the current paradigm shift in savanna management from a focus on single species conservation to protecting complete herbivore assemblages.

It is important that fire as a management tool is more focused on managing grassland heterogeneity than simply on burning moribund material in bunch grasslands, especially when the goal is conserving diverse grazer assemblages (Fuhlendorf and Engle 2001). Recent work showed that fire might even have a detrimental effect on some species by decreasing grazing lawn abundance (Archibald et al. 2005). In chapter 4 I also showed that fire might benefit some species, but not all, especially when compared with visitation to grazing lawns. The value of grazing lawns has long been neglected due to focus of burning practices on tall bunch grasslands, which is strongly influenced by experiences from livestock farming (Mentis et al. 1989). This influence of livestock rangeland management is also expressed in the still widely used system of increaser and decreaser grass species in South Africa (Dörgeleh 1999). Grazing lawn species are regarded as

increaser species (species that increase under high grazing pressure, Van Oudtshoorn 1999). A high percentage of increasers indicates that a site is overgrazed, which contradicts the ecological definition of grazing lawns. This shows that there is still a need to advocate the value of variation in grassland types. This might include, as was already indicated by Archibald et al. (2005), a redefinition of fire management protocols to account for a right balance of different grassland types.

It is obvious that the type of management actions one should take depend on the chosen conservation goals. However, for large herbivore conservation these goals are often poorly developed. We are in the midst of a changing paradigm from single species conservation to importance of conserving complete assemblages and herbivore diversity. While this paradigm is more and more adopted in management of African grazing systems, clearly defined goals are still rare. In other words, do we want evenness of abundance of large herbivore populations? Or do we focus on certain high profile species? Or on the highest species richness? What does a natural herbivore assemblage look like? As discussed in this thesis, spatial scale needs to be incorporated when trying to get insight in these questions. Even more importantly, as discussed in chapter 2, it is essential that monitoring programs are adapted to the new diversity paradigm to make them more suitable to measure (spatial) changes in species diversity.

Concluding and future challenge

In this thesis I presented some new ideas and empirical work on the partitioning of resources among large savanna grazers at different spatial scales. The most important message is that focusing on one spatial scale does not answer the question how so many grazer species can coexist. Resource partitioning does not simply seem to happen at one spatial scale. At the smallest scale species differed in their preference for resource grain within a grassland, one scale higher assemblages differ between grassland types and at an even large scale populations of species were differently distributed over the landscape. Or in other words, studying resource partitioning between wildebeest and zebra in the northern part of the park by estimating selected food species neglects the fact that this is probably a suboptimal wildebeest habitat, judging from their relative density distribution on a landscape scale. Most studies in the past were actually limited to one spatial scale. Our future challenge is that we need to design studies where we really integrate spatial scale in to our thinking about how herbivores partition the complex resource landscape.

Central to a better understanding of the role of scale is that we get a better idea of the continuous distribution of resources over the landscape, instead of depending on general classifications of resource quality and quantity (such as the lawn and bunch classes in this thesis). In this light, the development of new hyperspectral remote-sensing techniques looks promising and might allow us in the near future to map continuous resource distribution in detail at different scales

(Mutanga et al. 2005, Ferwerda 2005). At the same time new satellite collaring techniques allow us to get a much better idea about the exact spatial distribution of species and consequently the scales at which they respond to resource heterogeneity. The combination of these new techniques and the availability of conceptual models that include spatial scale to structure complex herbivore-resource systems might finally allow us to really get a grip on the mechanisms behind the coexistence of Africa's diverse herbivore species.



Compilation of the 6 focal species in this thesis,
drawn by Hilco Jansma....

Thobile, you joined our project in 2003-2004. Together with S'neh you formed a perfect couple to do botanical surveys. In 2004 you joined the South African police force. All the best with this new future...

References

- Archibald, S. and W. J. Bond. 2003. Modelling interactions between fire, rainfall and grazing. Pages 308-311 in Allsopp, N., A. R. Palmer, S. J. Milton, K. P. Kirkman, G. I. H. Kerley, C. R. Hurt, and C. J. Brown editors. International Rangelands Congress. Document Transformation Technologies, Durban, South Africa.
- Archibald, S., and W. J. Bond. 2004. Grazer movements: spatial and temporal responses to burning in a tall-grass African savanna. *International Journal of Wildland Fire* **13**: 1-9.
- Archibald, S., W. J. Bond, W. D. Stock, and D. H. K. Fairbanks. 2005. Shaping the landscape: fire-grazer interactions in an African savanna. *Ecological Applications* **15**: 96-109.
- Arsenault R., and N. Owen-Smith. 2002. Facilitation against competition in grazing herbivore assemblages. *Oikos* **97**: 313-318.
- Augustine, D. J., and S. J. McNaughton. 1998. Ungulate effects on the functional species composition of plant communities: Herbivore selectivity and plant tolerance. *Journal of Wildlife Management* **62**: 1165-1183.
- Augustine, D. J., S. J. McNaughton, and D. A. Frank. 2003. Feedbacks between soil nutrients and large herbivores in a managed savanna ecosystem. *Ecological Applications* **13**: 1325-1337.
- Bakker, E. S., H. Olff, M. Boekhoff, J. M. Gleichman, and F. Berendse. 2004. Impact of herbivores on nitrogen cycling: contrasting effects of small and large species. *Oecologia* **138**: 91-101.
- Bakker, E. S., M. E. Ritchie, H. Olff, D. G. Milchunas and J. M. H. Knops. Contrasting effects of large and small herbivores on plant species diversity along a productivity gradient. *Ecology Letters*, in press.
- Balmford A., P. Crane, A. Dobson, R. E. Green, and G. M. Mace. 2005. The 2010 challenge: data availability, information needs and extraterrestrial insights. *Philosophical Transactions of the Royal Society B* **360**: 221-228.
- Balmford, A., J. L. Moore, T. Brooks, N. Burgess, L. A. Hansen, P. Williams, and C. Rahbek. 2001. Conservation conflicts across Africa. *Science* **291**: 2616-2619.
- Barnes R. F. W. 2001. How reliable are dung counts for estimating elephant numbers? *African Journal of Ecology*, **39**:1-9.
- Barnes, J. I., C. Schier, and G. Van Rooy. 1999. Tourist's willingness to pay for wildlife viewing and wildlife conservation in Namibia. *South African Journal of Wildlife Research* **29**: 101-111.
- Barnosky, A. D., P. L. Koch, R. S. Feranec, S. L. Wing, and A. B. Shabel. 2004. Assessing the causes of Late Pleistocene extinctions on the continents. *Science* **306**: 70-75.
- Bell, R. H. V. 1970. The use of the herb layer by grazing ungulates in the Serengeti. Pages 111-124 in A. Watson editor. *Animal populations and relations to their food resources*. Blackwell, Oxford.
- Bell, R. H. V. 1971. A grazing ecosystem in the Serengeti. *Scientific American* **225**: 86-94.

-
- Belovsky, G. E. 1997. Optimal foraging and community structure: The allometry of herbivore food selection and competition. *Evolutionary Ecology* **11**: 641-672.
- Botha, M. S., and W. D. Stock. 2005. Stable isotope composition of faeces as an indicator of seasonal diet selection in wild herbivores in southern Africa. *South African Journal of Science* **101**: 371-374.
- Bothma J., M. J. S. Peel, S. Pettit, and D. Grossman. 1990. Evaluating the accuracy of some commonly used game-counting methods. *South African Journal of Wildlife Research* **20**: 26-32.
- Brashares J. S. and M. K. Sam. 2005. How much is enough? Estimating the minimum sampling required for effective monitoring of African reserves. *Biodiversity and Conservation*, **14**: 2709-2722.
- Brooks, P. M. 1982. Zebra, wildebeest and buffalo sub-population areas in the Hluhluwe-Corridor-Umfolozi Complex, Zululand, and their application in management. *South African Journal of Wildlife Research* **12**: 140-146.
- Brooks, P. M., and A. Berry. 1980. The responses of 18 ungulate species to fire in the central complex, Zululand, between October 1975 and September 1977. Ezemvelo KZN Wildlife, unpublished report, Pietermaritzburg.
- Brooks, P. M., and I. A. W. MacDonald. 1983. The Hluhluwe-Umfolozi Reserve: An ecological case history. Pages 51-57 in R. N. Owen-Smith, editor. *Management of large mammals in African conservation areas*. Haum Educational Publishers, Pretoria, Republic of South Africa.
- Brooks, S. 2005. Images of 'Wild Africa': nature tourism and the (re)creation of Hluhluwe game reserve, 1930-1945. *Journal of Historical Geography* **31**: 220-240.
- Brown, J. H., J. F. Gillooly, A. P. Allen, V. M. Savage and G. B. West. 2004. Toward a metabolic theory of ecology. *Ecology* **85**: 1771-1789.
- Bruinderink, G. W. T. A. G., D. R. Lammertsma, and E. Hazebroek. 2000. Effects of cessation of supplemental feeding on mineral status of red deer *Cervus elaphus* and wild boar *Sus scrofa* in the Netherlands. *Acta Theriologica* **45**: 71-85.
- Buckland S. T., D. R. Anderson, K. P. Burnham, and J. L. Laake. 1993. *Distance sampling: estimating abundance of biological populations*. Chapman and Hall, London.
- Bugalho, M. N. 1995. Food utilization and niche separation in large mammalian herbivores. *Revista de Ciencias Agrarias* **18**: 75-82.
- Carbone C., G. Cowlshaw, N. J. B. Isaac, and J. M. Rowcliffe. 2005. How far do animals go? Determinants of day range in mammals. *American Naturalist* **165**: 290-297.
- Carbone, C. and J. L. Gittleman. 2002. A common rule for the scaling of carnivore density. *Science* **295**: 2273-2276.
- Cargill, S. M., and R. L. Jefferies. 1984. The effects of grazing by lesser snow geese on the vegetation of a sub-arctic salt-marsh. *Journal of Applied Ecology* **21**: 669-686.
- Caro T. M. 1999. Conservation monitoring: estimating mammal densities in woodland habitats. *Animal Conservation*, **2**: 305-315.
- Caughley G. 1974. Bias in aerial survey. *Journal of Wildlife Management* **38**: 921-933.
- Caughley G., R. Sinclair, and D. Scottkennmis. 1976. Experiments in aerial survey. *Journal of Wildlife Management* **40**: 290-308.

- Cincotta, R. P., J. Wisniewski, and R. Engelman. 2000. Human population in the biodiversity hotspots. *Nature* **404**: 990-992.
- Clauss, M., R. Frey, B. Kiefer, M. Lechner-Doll, W. Loehlein, C. Polster, G. E. Rossner, and W. J. Streich. 2003. The maximum attainable body size of herbivorous mammals: morphophysiological constraints on foregut, and adaptations of hindgut fermenters. *Oecologia* **136**: 14-27.
- Coe, M. 1983. Large herbivores and food quality. Pages 345-368 in J. A. Lee, J. McNeill, and I. H. Rorison, editors. Nitrogen as an ecological factor. Blackwell Publishers, Oxford.
- Condit R., S. P. Hubbell, J. V. Lafrankie, R. Sukumar, N. Manokaran, R. B. Foster, and P. S. Ashton. 1996. Species-area and species-individual relationships for tropical trees: A comparison of three 50-ha plots. *Journal of Ecology*, **84**:549-562.
- Conway, A., D. Balfour, T. Dale, P. Hartley, P. Morrison, R. Howison, N. Galli, and M. Wadge. 2001. Hluhluwe-Umfolozi Park Management Plan. Unpublished report, Ezemvelo KZN Wildlife, Pietermaritzburg.
- Coppock D. L., J. K. Detling, J. E. Ellis, and M. I. Dyer. 1983a. Plant-herbivore interactions in a North American mixed-grass prairie. I. Effects of Black-Tailed Prairie Dogs on intraseasonal aboveground plant biomass and nutrient dynamics and plant species diversity. *Oecologia* **56**: 1-9.
- Coppock D. L., J. K. Detling, J. E. Ellis, and M. I. Dyer. 1983b. Plant-herbivore interactions in a North American mixed-grass prairie. II. Responses of Bison to modification of vegetation by Prairie Dogs. *Oecologia* **56**: 10-15
- Coppock, D. L., and J. K. Detling. 1986. Alteration of bison and black-tailed prairie dog grazing interaction by prescribed burning. *The Journal of Wildlife Management* **50**: 452-454.
- Coughenour, M. B. 1985. Graminoid responses to grazing by large herbivores: adaptations, exaptations, and interacting processes. *Annals of the Missouri Botanical Garden* **72**: 852-863.
- Coughenour, M. B. 1991. Spatial components of plant-herbivore interactions in pastoral, ranching, and native ungulate ecosystems. *Journal of Range Management* **44**: 530-542.
- Coughenour, M. B., and J. E. Ellis. 1993. Landscape and climatic control of woody vegetation in a dry tropical ecosystem: Turkana District, Kenya. *Journal of Biogeography* **20**: 383-398.
- Cromsigt, J. P. G. M., and H. Olf. Resource partitioning among savanna grazers mediated by local heterogeneity: an experimental approach. *Ecology*, in press.
- Cumming, D. H. M., and G. S. Cumming. 2003. Ungulate community structure and ecological processes: body size, hoof area and trampling in African savannas. *Oecologia* **134**:560-568.
- Danell, K., R. Bergstrom, P. Duncan and J. Pastor. 2006. Large herbivore ecology, ecosystem dynamics and conservation. Cambridge University Press, Cambridge.

-
- Danielsen F., N. D. Burgess, and A. Balmford. 2005. Monitoring matters: examining the potential of locally-based approaches. *Biodiversity and Conservation*, **14**: 2507-2542.
- Day T.A., and J. K. Detling. 1990. Grassland patch dynamics and herbivore grazing preference following urine deposition. *Ecology* **71**: 180-188
- Dekker, B., N. Van-Rooyen, and J. D. Bothma. 1996. Habitat partitioning by ungulates on a game ranch in the mopani veld. *South African Journal of Wildlife Research* **26**: 117-122.
- Demment, M. W. 1982. The scaling of ruminoreticulum size with body-weight in east-african ungulates. *African Journal of Ecology* **20**:43-47.
- Demment, M. W., and P. J. van Soest. 1985. A nutritional explanation for body-size patterns of ruminant and nonruminant herbivores. *American Naturalist* **125**: 641-672.
- Detling J. K. 1998. Mammalian herbivores: ecosystem-level effects in two grassland national parks. *Wildlife Society Bulletin* **26**: 438-448.
- Detling J. K., and E. L. Painter. 1983. Defoliation responses of western wheatgrass populations with diverse histories of prairie dog grazing. *Oecologia* **57**: 65-71
- Diamond J. 1996. *Guns, germs and steel: the fate of human societies*. W. W. Norton and company, London and New York.
- Dobson, A. P, and P. J. Hudson. 1986. Parasites, disease and the structure of ecological communities. *Trends in Ecology and Evolution* **1**: 11-15.
- Donkin, M. J., J. Pearce, and P. M. Chetty. 1993. *Methods for routine plant analysis in the ICFR laboratories*. Institute for Commercial Forestry Research, ICFR Bulletin Series no. 6/93, Pietermaritzburg, Republic of South Africa.
- Dörgeloh, W. G. 1999. Assessment of veld conditions with multivariate techniques in mixed bushveld, South Africa. *African Journal of Ecology* **37**: 194-201.
- Du Toit, J. T. 1990. Feeding-height stratification among African browsing ruminants. *African Journal of Ecology* **28**: 55-61.
- Du Toit, J. T. 1990. Home range – body mass relations: a field study on African browsing ruminants. *Oecologia* **85**: 301-303.
- Du Toit, J. T., and N. Owen-Smith. 1989. Body size, population metabolism and habitat specialization among large African herbivores. *American Naturalist* **133**: 736-740.
- Du Toit, J. T., K. H. Rogers and H. C. Biggs. 2003. *The Kruger experience: ecology and management of savanna heterogeneity*. Island Press, Washington, D.C.
- Duncan, P., T. J. Foose, I. J. Gordon, C. G. Gakahu, and M. Lloyd. 1990. Comparative nutrient extraction from forages by grazing bovids and equids: a test of the nutritional model of equid/bovid competition and coexistence. *Oecologia* **84**: 411-418.
- Du-Toit, J. T., and D. H. M. Cumming. 1999. Functional significance of ungulate diversity in African savannas and the ecological implications of the spread of pastoralism. *Biodiversity and Conservation* **8**: 1643-1661.
- Du-Toit, J. T., and N. Owen-Smith. 1989. Body size, population metabolism, and habitat specialization among large African herbivores. *American Naturalist* **133**: 736-740.

- East R. 1984. Rainfall, Soil Nutrient Status and Biomass of Large African Savanna Mammals. *African Journal of Ecology* **22**: 245-270.
- ESRI 2003. ArcView 8.3, Redlands, California.
- ESRI. 2004. ArcMap 9.0. Redlands, California.
- Esty, A. 2005. Investigating a mega-mystery - Two recent studies try to help unravel the causes of late Pleistocene extinctions. *American Scientist* **93**: 408-409.
- Farnsworth, K. D., S. Focardi, and J. A. Beecham. 2002. Grassland-Herbivore interactions: how do grazers coexist? *American Naturalist* **159**: 24-39.
- Ferwerda, J. G. 2005. Charting the quality of forage. Mapping and measuring the variation of chemical components in foliage with hyperspectral remote sensing. Dissertation, ITC, Enschede.
- Fisher R. A., A. S. Corbett, and C. B. Williams. 1943. The relation between the number of species and the number of individuals in a random sample of an animal population. *Journal of Animal Ecology* **12**: 42-58.
- Fox, B. J. and M. D. Fox. 2000. Factors determining mammal species richness on habitat islands and isolates: habitat diversity, disturbance, species interactions and guild assembly rules. *Global Ecology and Biogeography* **9**: 19-37.
- Frank D. A., S. J. McNaughton, and B. F. Tracy. 1998. The ecology of the earth's grazing ecosystems. *BioScience* **48**: 513-521.
- Fritz H., and P. Duncan. 1994. On the Carrying-Capacity for Large Ungulates of African Savanna Ecosystems. *Proceedings of the Royal Society of London Series B* **256**: 77-82.
- Fryxell J. M., J. F. Wilmshurst, A. R. E. Sinclair, D. T. Haydon, R. D. Holt, and P. A. Abrams. 2005. Landscape scale, heterogeneity, and the viability of Serengeti grazers. *Ecology Letters* **8**: 328-335.
- Fryxell, J. M., J. F. Wilmshurst, and A. R. E. Sinclair. 2004. Predictive models of movement by Serengeti grazers. *Ecology* **85**: 2429-2435.
- Fuhlendorf, S. D., and D. M. Engle. 2001. Restoring heterogeneity on rangelands: ecosystem management based on evolutionary grazing patterns. *BioScience* **51**: 625-632.
- Gaidet N., H. Fritz, S. Messad, S. Mutake, and S. Le Bel. 2005. Measuring species diversity while counting large mammals: comparison of methods using species-accumulation curves. *African Journal of Ecology*, **43**:56-63.
- Gause G. F. 1934. *The struggle for existence*, Williams and Wilkins, Baltimore.
- Gautier, A. 1998. *De gouden kooi. Over het ontstaan van het huisdier*. Uitgeverij Hadewijch, Antwerpen.
- Geist, V. 1974. On the relationship of social evolution and ecology in ungulates. *American Zoologist* **14**: 205-220.
- Gillooly, J. F., J. H. Brown, G. B. West, V. M. Savage, and E. L. Charnov. 2001. Effects of size and temperature on metabolic rate. *Science* **293**:2248-2251.
- Gillson, L. 2004. Evidence of hierarchical patch dynamics in an east African savanna? *Landscape Ecology* **19**: 883-894.

-
- Gonzalez-Megias, A., J. M. Gomez, and F. Sanchez-Pinero. 2004. Effects of ungulates on epigeal arthropods in Sierra Nevada National Park (southeast Spain). *Biodiversity and Conservation* **13**:733-752.
- Gordon, I. J., A. J. Hester, and M. Festa-Bianchet. 2004. The management of wild herbivores to meet economic, conservation and environmental objectives. *Journal of Applied Ecology* **41**: 1021-1031.
- Gordon, I. J., and A. W. Illius. 1996. The nutritional ecology of African ruminants: a reinterpretation. *Journal of Animal Ecology* **65**: 18-28.
- Gordon, I. J., and A. W. Illius. 1994. The functional significance of the browser-grazer dichotomy in African ruminants. *Oecologia* **98**:167-175.
- Grange, S., P. Duncan, J. M. Gaillard, A. R. E. Sinclair, P. J. P. Gogan, C. Packer, H. Hofer, and M. East. 2004. What limits the Serengeti zebra population? *Oecologia* **140**: 523-532.
- Hamilton, E. W., S. J. McNaughton, and J. S. Coleman. 2001. Molecular, Physiological, and growth responses to sodium stress in C4 grasses from a soil salinity gradient in the Serengeti ecosystem. *American Journal of Botany* **88**: 1258-12656.
- Hansen, R. M., M. M. Mugambi, and S. M. Bauni. 1985. Diets and Trophic Ranking of Ungulates of the Northern Serengeti. *Journal of Wildlife Management* **49**:823-829.
- Hardin G. 1960. Competitive Exclusion Principle. *Science* **131**: 1292-1297.
- Haskell, J. P., M. E. Ritchie, and H. Olf. 2002. Fractal geometry predicts varying body size scaling relationships for mammal and bird home ranges. *Nature* **418**: 527-530.
- Hellgren, E. C., and W. J. Pitts. 1997. Sodium economy in white-tailed deer (*Odocoileus virginianus*). *Physiological zoology* **70**: 547-555.
- Hester A. J., I. J. Gordon, G. J. Baillie, and E. Tappin. 1999. Foraging behaviour of sheep and red deer within natural heather grass mosaics. *Journal of Applied Ecology* **36**: 133-146.
- Hester A. J., and G. J. Baillie. 1998. Spatial and temporal patterns of heather use by sheep and red deer within natural heather/grass mosaics. *Journal of Applied Ecology* **35**: 772-784
- Hik D. S. and R. L. Jefferies. 1990. Increases in the net aboveground primary production of a salt-marsh forage grass - a test of the predictions of the herbivore-optimization model. *Journal of Ecology* **78**: 180-195.
- HillierLambers R., M. Rietkerk, F. van den Bosch, H. H. T. Prins, and H. de Kroon. 2001. Vegetation pattern formation in semi-arid grazing systems. *Ecology* **82**: 50-61
- Hirst, S. M. 1975. Ungulate-habitat relationships in a south african woodland/savanna ecosystem. *Wildlife Monographs* **44**: 1-60.
- Hobbs, N. T. 1996. Modification of ecosystems by ungulates. *Journal of Wildlife Management* **60**: 695-713.
- Hobbs, N. T., and K. R. Searle. 2005. A reanalysis of the body mass scaling of trampling by large herbivores. *Oecologia* **145**: 462-464.
- Hofmann, R. R. 1989. Evolutionary steps of ecophysiological adaptation and diversification of ruminants. A comparative view of their digestive system. *Oecologia* **78**: 443-457.

- Hofmann, R. R., and D. R. M. Stewart. 1972. Grazer or browser: a classification based on the stomach structure and feeding habits of East African ruminants. *Mammalia* **36**: 226-240.
- Holdo R. M., L. R. McDowell. 2004. Termite mounds as nutrient-rich food patches for elephants. *Biotropica* **36**: 231-239
- Holland, E. A., and J. K. Detling. 1990. Plant-response to herbivory and belowground nitrogen cycling. *Ecology* **71**: 1040-1049.
- Hopcraft, J. G. C., A. R. E. Sinclair, and C. Packer. 2005. Planning for success: Serengeti lions seek prey accessibility rather than abundance. *Journal of Animal Ecology* **74**: 559-566.
- Huisman J., and H. Olff. 1998. Competition and facilitation in multispecies plant-herbivore systems of productive environments. *Ecology Letters* **1**: 25-29
- Illius, A. W., and I. J. Gordon. 1992. Modelling the nutritional ecology of ungulate herbivores: evolution of body size and competitive interactions. *Oecologia* **89**: 428-434.
- Illius, A. W., and T. G. O'Connor. 1999. On the relevance of nonequilibrium concepts to arid and semiarid grazing systems. *Ecological Applications* **9**: 798-813.
- Illius, A. W., and T. G. O'Connor. 2000. Resource heterogeneity and ungulate population dynamics. *Oikos* **89**: 283-294.
- Jachmann H. 1991. Evaluation of four survey methods for estimating elephant densities. *African Journal of Ecology* **29**: 188-195.
- Jachmann, H. 2002. Comparison of aerial counts with ground counts for large African herbivores. *Journal of Applied Ecology* **39**: 841-852.
- Jacobs P. 2002. Methods for determining herbivore abundance in savannas: dung and tracks. Thesis, Wageningen University, Wageningen, The Netherlands.
- Jarman, P. J. 1974. Social organization of antelope in relation to their ecology. *Behaviour* **48**: 215-267.
- Jarman, P. J. 1970. Attachment to home area in impala. *East African Wildlife Journal* **8**: 198-200.
- Jarman, P. J. 1971. Diets of large mammals in the woodlands around Lake Kariba, Rhodesia. *Oecologia* **8**: 157-178.
- Jetz W., C. Carbone, J. Fulford, and J. H. Brown. 2004. The scaling of animal space use. *Science* **306**: 266-268.
- Johnson, C. N. 2002. Determinants of loss of mammal species during the Late Quaternary 'megafauna' extinctions: life history and ecology, but not body size. *Proceedings of the Royal Society of London Series B* **269**: 2221-2227.
- Jones J. A. 1990. Termites, soil fertility and carbon cycling in dry tropical Africa – a hypothesis. *Journal of Tropical Ecology* **6**: 291-305.
- King, L. 1970. The geology of Hluhluwe Game Reserve. *Petros* **2**: 16-19.
- Kingdon, J. 2001. *The Kingdon field guide to African mammals*. Academic press, San Diego.
- Kleiber, M. 1932. Body size and metabolism. *Hilgardia* **6**: 315-353.
- Kleiber, M. 1961. *The fire of life: an introduction to animal energetics*. Wiley, New York, U.S.A.

-
- Kroger, R., and K. H. Rogers. 2005. Roan (*Hippotragus equinus*) population decline in Kruger National Park, South Africa: influence of a wetland boundary. *European Journal of Wildlife Research* **51**: 25-30.
- Lamprey, H. F. 1963. Ecological separation of the large mammal species in the Tarangire Game Reserve, Tanganyika. *East African Wildlife Journal* **1**: 63-92.
- Lamprey, R. H., and R. S. Reid. 2004. Expansion of human settlement in Kenya's Maasai Mara: what future for pastoralism and wildlife? *Journal of Biogeography* **31**: 997-1032.
- Leus, K., and A. A. MacDonald. 1997. From babirusa (*Babyrousa babyrussa*) to domestic pig: the nutrition of swine. *Proceedings of the Nutrition Society* **56**: 1001-1012.
- Loibooki, M., H. Hofer, K. L. I. Campbell, and M. L. East. 2002. Bushmeat hunting by communities adjacent to the Serengeti National Park, Tanzania: the importance of livestock ownership and alternative sources of protein and income. *Environmental Conservation* **29**:391-398.
- Londo G. 1976. The decimal scale for relevés of permanent quadrats. *Vegetatio* **33**: 61-64.
- Ludwig, F., H. de Kroon, F. Berendse, and H. H. T. Prins. 2004. The influence of savanna trees on nutrient, water and light availability and the understorey vegetation. *Plant Ecology* **170**: 93-105.
- Magurran A. E. 1988. *Ecological diversity and its measurement*. Chapman and Hall, London.
- Magurran, A. E. 2004. *Measuring Biological Diversity*. Blackwell Publishing, Oxford.
- Manly, B. F. J., L. L. McDonald, D. L. Thomas, T. L. McDonald, and W. P. Erickson. 2002. *Resource selection by animals*. Kluwer Academic Publishers, Dordrecht.
- Manson, A. D., and V. G. Roberts. 2000. *Analytical methods used by the soil fertility and analytical services section*. Kwazulu-Natal Department of Agriculture and Environmental Affairs, KZN AGRI-REPORT No. N/A/2001/4, Pietermaritzburg.
- McNaughton S. J. 1985. Ecology of a grazing ecosystem: the Serengeti. *Ecological Monographs*, **55**: 259-294.
- McNaughton S. J. 1983b. Compensatory growth as a response to herbivory. *Oikos* **40**: 329-336.
- McNaughton, S. J. 1976. Serengeti Migratory Wildebeest - Facilitation of Energy-Flow by Grazing. *Science* **191**: 92-94.
- McNaughton, S. J. 1979. Grazing as an optimization process - grass ungulate relationships in the Serengeti. *American Naturalist* **113**: 691-703.
- McNaughton, S. J. 1983a. Serengeti grassland ecology: the role of composite environmental factors and contingency in community organization. *Ecological Monographs* **53**: 291-320.
- McNaughton, S. J. 1984. Grazing lawns: animals in herds, plant form, and coevolution. *American Naturalist* **124**: 863-886.
- McNaughton, S. J. 1988. Mineral nutrition and spatial concentrations of African ungulates. *Nature* **334**: 343-345.
- McNaughton, S. J. 1990. Mineral nutrition and seasonal movements of African migratory ungulates. *Nature* **345**: 613-615.

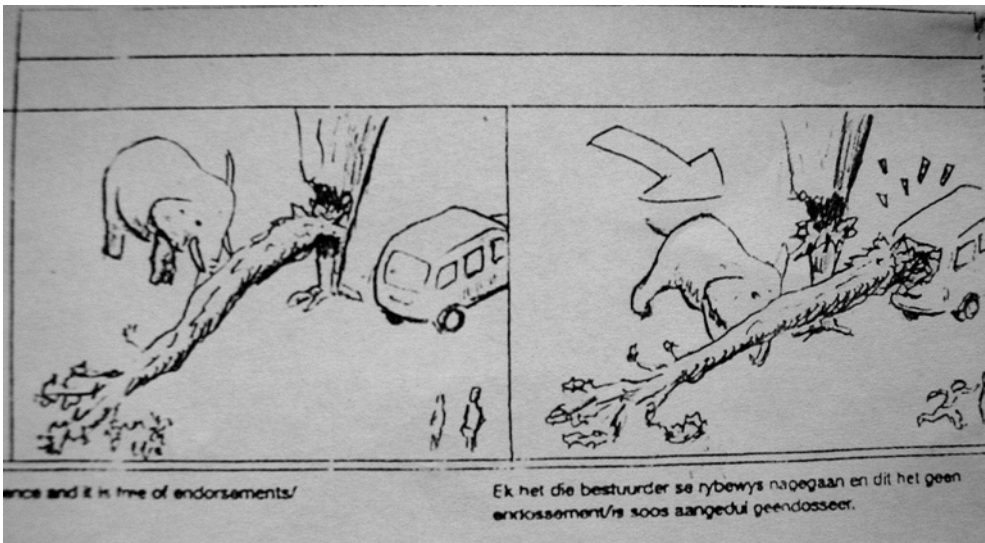
- McNaughton, S. J. 1993. Biodiversity and function of grazing ecosystems. Pages 361-383 in Schulze, E. D. and H. A. Mooney, editors. Biodiversity and ecosystem functioning. Springer, Berlin.
- McNaughton, S. J., and N. J. Georgiadis. 1986. Ecology of grazing and browsing mammals. *Annual Review of Ecology and Systematics* **17**: 39-66.
- McNaughton, S. J., F. F. Banyikwa, and M. M. McNaughton. 1997. Promotion of the cycling of diet-enhancing nutrients by African grazers. *Science* **278**: 1798-1800.
- Melton, D. A. 1987. Habitat selection and resource scarcity. *South African Journal of Science* **83**: 646-651.
- Mentis, M. T., D. Grossman, M. B. Hardy, T. G. O'Connor, and P. J. O'Reagain. 1989. Paradigm shifts in South African science, management and administration. *South African Journal of Science* **85**: 684-687.
- Meyer, B. 1999. Supervised LANDSAT-TM mapping of the spatially heterogeneous savanna of Hluhluwe-Umfolozi Park. Thesis, Ludwig-Maximilians-Universität, München.
- Milchunas, D. G., W. K. Lauenroth, and I. C. Burke. 1998. Livestock grazing: animal and plant biodiversity of shortgrass steppe and the relationship to ecosystem function. *Oikos* **83**: 65-74.
- Milchunas, D. G., W. K. Lauenroth, and O. E. Sala. 1988. A generalized model of the effects of grazing by large herbivores on grassland community structure. *American Naturalist* **132**: 87-106.
- Milner-Gulland, E. J., and E. L. Bennett. 2003. Wild meat: the bigger picture. *Trends in Ecology & Evolution* **18**: 351-357.
- Mobaek R., A. K. Narmo, and S. R. Moe. 2005. Termitaria are focal feeding sites for large ungulates in Lake Mburo National Park, Uganda. *Journal of Zoology* **267**: 97-102
- Moe, S. R., P. Wegge, and E. B. Kapela. 1990. The influence of man-made fires on large wild herbivores in Lake Burungi area in northern Tanzania. *African Journal of Ecology* **28**: 35-43.
- Moran, P. A. P. 1948. The interpretation of statistical maps. *Journal of the Royal Statistical Society B* **10**: 243-251.
- Murray M. G., and D. Brown. 1993. Niche Separation of Grazing Ungulates in the Serengeti - An Experimental Test. *Journal of Animal Ecology* **62**: 380-389.
- Murray, M. G., and A. W. Illius. 2000. Vegetation modification and resource competition in grazing ungulates. *Oikos* **89**: 501-508.
- Mutanga, O., A. K. Skidmore, L. Kumar, and J. G. Ferwerda. 2005. Estimating tropical pasture quality at canopy level using band depth analysis with continuum removal in the visible domain. *International Journal of Remote Sensing* **26**: 1093-1108.
- Newmark, W. D. 1996. Insularization of Tanzanian parks and the local extinction of large mammals. *Conservation Biology* **10**:1549-1556.
- Norton-Griffiths M. 1978. Counting animals. Handbook No 1. Techniques currently used in African wildlife ecology. African Wildlife Foundation, Nairobi.
- Oindo, B. O., A. K. Skidmore, and P. De Salvo. 2003. Mapping habitat and biological diversity in the Maasai Mara ecosystem. *International Journal of Remote Sensing* **24**: 1053-1069.

-
- Olff, H., and M. E. Ritchie. 2001. Fragmented nature: consequences for biodiversity. *Landscape and Urban Planning* **58**: 83-92.
- Olff, H., and M. E. Ritchie. 1998. Effects of herbivores on grassland plant diversity. *Trends in Ecology and Evolution* **13**: 261-265.
- Olff, H., M. E. Ritchie, and H. H. T. Prins. 2002. Global environmental controls of diversity in large herbivores. *Nature* **415**: 901-904.
- Owen-Smith, N. 1987. Pleistocene extinctions - the pivotal role of megaherbivores. *Paleobiology* **13**: 351-362.
- Owen-Smith, N. 1988. *Megaherbivores: the influence of very large body size on ecology*. Cambridge University Press, Cambridge.
- Owen-Smith, N. 2004. Functional heterogeneity in resources within landscapes and herbivore population dynamics. *Landscape Ecology* **19**: 761-771.
- Peel M. J. S., and J. D. Bothma. 1995. Comparison of the accuracy of 4 methods commonly used to count impala. *South African Journal of Wildlife Research* **25**: 41-43.
- Perrin, M. R., and R. Brereton-Stiles. 1999. Habitat use and feeding behaviour of the buffalo and the white rhinoceros in the Hluhluwe-Umfolozi Game Reserve. *South African Journal of Wildlife Research* **29**: 72-80.
- Person B. T., M. P. Herzog, R. W. Ruess, J. S. Sedinger, R. M. Anthony, and C. A. Babcock. 2003. Feedback dynamics of grazing lawns: coupling vegetation change with animal growth. *Oecologia* **135**: 583-592
- Peters, R.H. 1983. *The ecological implications of body size*. Cambridge University Press, Cambridge.
- Pielou E. C. 1975. *Ecological Diversity*. John Wiley and Sons, New York.
- Prins, H. H. T. 1992. The pastoral road to extinction: competition between wildlife and traditional pastoralism in East Africa. *Environmental Conservation* **19**: 117-123.
- Prins, H. H. T., and G. R. Iason. 1989. Dangerous lions and nonchalant buffalo. *Behaviour* **108**: 262-296.
- Prins, H. H. T., and H. Olff. 1998. Species-richness of african grazer assemblages: towards a functional explanation. Pages 449-490 *in* D. M. Newbery, H. H. T. Prins, and N. D. Brown editors. *Dynamics of tropical communities*. Blackwell, Oxford.
- Prins, H. H. T., and H. P. van der Jeugd. 1993. Herbivore population crashes and woodland structure in East Africa. *Journal of Ecology* **81**: 305-314.
- Prins, H. H. T., J. J. Grootenhuis and T. T. Dolan. 2000. *Wildlife conservation by sustainable use*. Kluwer Academic Publishers, Dordrecht.
- Redfern, J. V., R. Grant, H. Biggs, and W. M. Getz. 2003. Surface-water constraints on herbivore foraging in the Kruger National Park, South Africa. *Ecology* **84**: 2092-2107.
- Reilly B. K. and C. I. Haskins. 1999. Comparative efficiency of two game counting techniques as applied to Suikerbosrand Nature Reserve. *South African Journal of Wildlife Research*, **29**: 89-97.
- Rietkerk M., S. C. Dekker, P. C. de Ruiter, and J. van den Koppel. 2004. Self-organized patchiness and catastrophic shifts in ecosystems. *Science* **305**: 1926-1929

- Ritchie, M. E., and H. Olff. 1999. Spatial scaling laws yield a synthetic theory of biodiversity. *Nature* **400**: 557-560.
- Ritchie, M. E., and H. Olff. 2004. Resource partitioning and biodiversity in fractal environments, with application to dryland communities. Pages 206-219 in M. Shachak, J. R. Gosz, A. Perevolotsky, and S. T. A. Pickett, editors. *Biodiversity in drylands: towards a unified framework*. Oxford University Press, Oxford, UK.
- Ritchie, M. E., D. Tilman, and J. M. H. Knops. 1998. Herbivore effects on plant and nitrogen dynamics in oak savanna. *Ecology* **79**: 165-177.
- Robbins, C. T. 1993. *Wildlife feeding and nutrition*. Second edition, Academic Press, San Diego.
- Ruess R. W., D. D. Uliassi, C. P. H. Mulder, and B. T. Person. 1997. Growth responses of *Carex ramenskii* to defoliation, salinity, and nitrogen availability: Implications for geese-ecosystem dynamics in western Alaska. *Ecoscience* **4**: 170-178.
- Ruess, R. W., and S. J. McNaughton. 1984. Urea as a promotive coupler of plant-herbivore interactions. *Oecologia* **63**: 331-337.
- Ruess, R. W., S. J. McNaughton, and M. B. Coughenour. 1983. The effects of clipping, nitrogen-source and nitrogen concentration on the growth-responses and nitrogen uptake of an east-African sedge. *Oecologia* **59**: 253-261.
- Savage, V. M., J. F. Gillooly, W. H. Woodruff, G. B. West, A. P. Allen, B. J. Enquist, and J. H. Brown. 2004. The predominance of quarter-power scaling in biology. *Functional ecology* **18**: 257-282.
- Schulze, R. E. 1997. *South African Atlas of Agrohydrology and – Climatology*. Water Research Commission, Report TT82/96, Pretoria.
- Semple W. S., I. A. Cole, and T. B. Koen. 2003. Performance of some perennial grasses on severely salinised sites on the inland slopes of New South Wales. *Australian Journal of Experimental Agriculture* **43**: 357-371.
- Sinclair, A. R. E. 1985. Does interspecific competition or predation shape the african ungulate community? *Journal of Animal Ecology* **54**: 899-918.
- Sinclair, A. R. E., S. Mduma, and J. S. Brashares. 2003. Patterns of predation in a diverse predator-prey system. *Nature* **425** : 288-290.
- Smil, V. 2000. Laying down the law. *Nature* **403**: 597.
- Stalmans M., K. Balkwill, E. T. F. Witkowski, and K. H. Rogers. 2001. A Landscape Ecological Approach to Address Scaling Problems in Conservation Management and Monitoring. *Environmental Management*, **28**: 389-401.
- Surovell, T., N. Waguespack, and P. J. Brantingham. 2005. Global archaeological evidence for proboscidean overkill. *Proceedings of the National Academy of Sciences of the United States of America* **102**: 6231-6236.
- Swemmer T. 1998. *The distribution and ecology of grazing lawns in a South African savanna ecosystem*. Thesis, University of Cape Town, Cape Town
- Tomor, B. M., and N. Owen-Smith. 2002. Comparative use of grass regrowth following burns by four ungulate species in the Nylsvley Nature Reserve, South Africa. *African Journal of Ecology* **40**: 201-204.

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- Trueman, C. N. G., J. H. Field, J. Dortch, B. Charles, and S. Wroe. 2005. Prolonged coexistence of humans and megafauna in Pleistocene Australia. *Proceedings of the National Academy of Sciences of the United States of America* **102**: 8381-8385.
- Underwood, R. 1982. Vigilance behaviour in grazing African antelopes. *Behaviour* **79**: 82-107.
- Underwood, R. 1983. The feeding behaviour of grazing African ungulates. *Behaviour* **84**: 195-243.
- Van de Vijver, C. A. D. M. 1999. Fire and life in Tarangire: the effects of burning and herbivory on an East African savanna system. Dissertation, Wageningen University, Wageningen.
- Van Langevelde F., C. A. D. M. van de Vijver, L. Kumar, J. van den Koppel, N. de Ridder, J. van Andel, A. K. Skidmore, J. W. Hearne, L. Stroosnijder, W. J. Bond, H. H. T. Prins, and M. Rietkerk. 2003. Effects of fire and herbivory on the stability of savanna ecosystems. *Ecology* **84**: 337-350.
- Van Oudtshoorn, F. P. 1999. Guide to grasses of Southern Africa. Briza Publications, Pretoria.
- Van Wieren, S. E. 1996. Digestive strategies in ruminants and non-ruminants. Dissertation, Wageningen University, Wageningen.
- Vesey-Fitzgerald, D. F. 1960. Grazing succession among East African game animals. *Journal of Mammalogy* **41**: 161-172.
- Voeten, M.M., and H. H. T. Prins. 1999 Resource partitioning between sympatric wild and domestic herbivores in the Tarangire region of Tanzania. *Oecologia* **120**: 287-294.
- Wallis de Vries M. F., E. A. Laca, and M. W. Demment. 1999. The importance of scale of patchiness for selectivity in grazing herbivores. *Oecologia* **121**: 355-363.
- Wang, W., B. Vinocur, and A. Altman. 2003. Plant responses to drought, salinity and extreme temperatures: towards genetic engineering for stress tolerance. *Planta* **218**: 1-14.
- West, G. B., J. H. Brown, and B. J. Enquist. 1997. A general model for the origin of allometric scaling laws in biology. *Science* **276**: 122-126.
- Whateley A., and R. N. Porter. 1983. The woody vegetation communities of the Hluhluwe-Corridor-Umfolozi Game Reserve Complex. *Bothalia* **14**: 745-758.
- Wilmshurst J. F., J. M. Fryxell, B. P. Farm, A.-R. E. Sinclair, and C. P. Henschel. 1999. Spatial distribution of Serengeti wildebeest in relation to resources. *Canadian Journal of Zoology* **77**: 1223-1232.
- Wilmshurst, J. F., J. M. Fryxell, and C. M. Bergman. 2000. The allometry of patch selection in ruminants. *Proceedings of the Royal Society of London Series B* **267**: 345-349.
- Wilmshurst, J. F., J. M. Fryxell, and R. J. Hudson. 1995. Forage quality and patch choice by wapiti (*Cervus elaphus*). *Behavioral Ecology* **6**: 209-217.
- Wilsey, B. J. 1996. Variation in use of green flushes following burns among African ungulate species: The importance of body size. *African Journal of Ecology* **34**: 32-38.
- Wilson D. E., F. R. Cole, J. D. Nichols, R. Rudran, and M. S. Foster. 1996. Measuring and monitoring biological diversity: standard methods for mammals. Smithsonian Institution Press, Washington, DC.

- Woolnough A. P., and J. T. du Toit. 2001. Vertical zonation of browse quality in tree canopies exposed to a size-structured guild of African browsing ungulates. *Oecologia* **129**: 585-590.
- Wu, J. G., and O. L. Loucks. 1995. From balance of nature to hierarchical patch dynamics: A paradigm shift in ecology. *Quarterly Review of Biology* **70**: 439-466.
- Young, T. P., N. Partridge, and A. Macrae. 1995. Long-term glades in Acacia bushland and their edge effects in Laikipia, Kenya. *Ecological Applications* **5**: 97-108.



Fragment of a police report, drawn by Hilco Jansma, illustrating how an elephant managed to damage one of our field cars while trying to chase the people in the lower right corner.

Samenvatting

Grote grazers behoren tot de meest in het oog springende soortengroepen van het zoogdierenrijk. De meest diverse gemeenschappen van deze grote grazers kunnen worden aangetroffen op het Afrikaanse continent. Gemeenschappen met wel 10 verschillende soorten grazers kunnen lokaal samenlevend waargenomen worden, allen met gras als dominante voedselbron. Deze diverse grazergemeenschappen en hun leefsysteem zijn van grote socio-economische en ecologische waarde. De invloed van grote grazers op de mens is enorm geweest tijdens onze evolutionaire geschiedenis en hoewel gedomesticeerde grazers het grootste deel van de socio-economische rol van hun wilde metgezellen hebben overgenomen in de geïndustrialiseerde samenlevingen, spelen deze wilde grazers nog steeds een cruciale rol in veel Afrikaanse landen. Dit is zowel een directe rol als bron van eiwitten als een indirecte rol als belangrijke motor van de sterk groeiende toerisme industrie. Naast deze socio-economische rol is de potentiële invloed van grote grazers op hun leefsysteem ook enorm, van het in gang zetten van grootschalige vegetatieveranderingen tot het beïnvloeden van nutriënten cycli. Doordat ze op deze manier de systemen vormen waarin ze leven beïnvloeden ze ook het leefmilieu van vele andere soorten die van deze systemen afhankelijk zijn (van insecten, tot vogels en roofdieren). Bovendien groeit het aantal studies dat het belang benadrukt van de soortenrijkdom van grazergroepen, omdat soorten elkaar aanvullen in de manier waarop ze het systeem beïnvloeden.

Het is alarmerend om te beseffen dat deze diverse grazer gemeenschappen en hun ecologische en socio-economische rol steeds meer bedreigd worden. Vrij rondzwervende grote grazers zijn reeds verdwenen uit grote delen van Afrika en de overblijvende gebieden met hoge soortenrijkdom vallen grotendeels samen met de regio's met de sterkste menselijke bevolkingstoename, waardoor het mens-dier conflict alleen nog maar meer zal toenemen. Om de diverse grazer gemeenschappen en hun functionele rol te beschermen voor de toekomst is daarom een sterke behoefte aan kennis over de factoren die de soortenrijkdom en populatieaantallen van deze gemeenschappen bepalen. Hoewel ook andere aspecten zoals predatie en gevoeligheid voor ziekten van belang kunnen zijn, wordt de soortenrijkdom van grote grazers over het algemeen verklaard door de hypothese dat de grazer soorten verschillen in hun gebruik van de gedeelde voedselbron gras. Deze hypothese komt voort uit het 'uitsluitel principe' dat soorten niet naast elkaar kunnen voortbestaan als ze één voedselbron op dezelfde manier gebruiken, omdat de ene soort de andere zal wegconcurreren. Verschillende studies hebben in het verleden benadrukt dat het lichaamsgewicht van een soort een belangrijke eigenschap is die de verschillen tussen soorten in voedselgebruik bepaalt omdat deze eigenschap de optimale kwaliteit en kwantiteitverhouding van zijn voedsel beïnvloedt, waarbij zwaardere soorten een lagere voedselkwaliteit kunnen tolereren dan kleinere soorten. Voorwaarde voor dit idee is dat er in het leefmilieu voldoende variatie in voedselkwaliteit en -kwantiteit

(voedselheterogeniteit) aanwezig is voor soorten om het voedsel onderling te verdelen. Tot nu toe, in de Afrikaanse context, is voedselheterogeniteit vooral onderzocht als variatie in plantensoorten en vegetatiestructuur, met name grashoogte en blad-stengel verhouding. Bovendien hebben studies uit oost Afrika laten zien dat grazers hun voedsel verdelen in de tijd. Verschillende soorten gebruiken dezelfde gebieden en dezelfde plantensoorten maar op verschillende tijdstippen tijdens grootschalige migraties. In veel gebieden vinden echter geen grootschalige migraties (meer) plaats (zoals in veel Zuid-Afrikaanse reservaten). Toch herbergen deze gebieden bijzonder soortenrijke grazergemeenschappen zonder aanwijzingen van competitie tussen soorten of achteruitgang van populatieaantallen. Duidelijk empirisch bewijs hoe grazer soorten in deze gebieden hun voedsel verdelen ontbreekt.

In dit proefschrift beargumenteer ik dat dit gebrek aan bewijs (gedeeltelijk) komt doordat de ruimtelijke component onderbelicht is gebleven in ons denken over voedselverdeling door grote grazers. Ruimtelijke variatie in voedselkwaliteit en -kwantiteit kan worden gedefinieerd op verschillende schalen, van het niveau van een foerageerplek tot grootschalige landschapsgradiënten. Vroegere studies hebben het effect van ruimtelijke voedselheterogeniteit bestudeerd op het foerageergedrag van een enkele soort en een aantal modelmatige studies hebben een relatie gelegd tussen deze heterogeniteit en de stabiliteit van populatieaantallen van grote grazers. Er is echter een gebrek aan empirische studies die specifiek testen hoe ruimtelijke voedselheterogeniteit de verdeling van dit voedsel tussen verschillende soorten kan bevorderen en uiteindelijk kan bijdragen aan de coëxistentie van deze soorten. Het doel van dit proefschrift is dan ook om empirisch bewijs te verzamelen voor de rol van het ruimtelijk verdelen van voedsel voor de coëxistentie van grote Afrikaanse grazers door het doen van zowel observationeel als experimenteel onderzoek op verschillende schalen. Alle studies zijn uitgevoerd in Hluhluwe-iMfolozi park, een 90,000 ha groot reservaat aan de oostkust van Zuid-Afrika, net ten zuiden van Swaziland. De studies hebben zich met name gericht op de zes meest voorkomende grote grazers in dit park; impala, wrattenzwijn, wildebeest, zebra, Afrikaanse buffel en witte neushoorn. Ik begin met beschrijven hoe het lichaamsgewicht de verspreiding van deze zes soorten over het park beïnvloedt en hoe deze verspreiding gerelateerd is aan landschappelijke variatie in habitatype en -kwaliteit (hoofdstuk 3). De zwaardere soorten waren meer gelijkmatig verdeeld over het landschap dan de lichtere grazer soorten en hadden een meer diverse habitat gebruik, hoewel deze relatie sterk werd beïnvloed door de verteringsfysiologie van de verschillende soorten. De relatie was sterk voor herkauwers maar zwak tot afwezig voor niet-herkauwers. Doordat grote en kleinere grazer soorten zich op een verschillende manier over het landschap verspreiden verdelen ze hun voedsel wellicht (deels) op landschappelijke schaal. Op een fijnere schaal (hectares) veroorzaken verschillen in bodemtypen ruimtelijke variatie in graslandtypen. Op deze schaal beschrijf ik hoe grazer soorten zich verdelen over deze graslandtypen, die verschillen in algemene voedselkwaliteit en -kwantiteit, en

hoe vuur deze verdeling tijdelijk kan beïnvloeden (hoofdstuk 4). Ik maak een onderscheid tussen *grazing lawn* graslanden, getypeerd door korte stolonifere grassen en gesitueerd op relatief zandige bodems en *bunch grass* graslanden, bestaande uit hoog opgroeiende grassoorten en gesitueerd op de meer kleiige bodems. In het algemeen vormden de *grazing lawns* nutriënten hotspots die alle grazer soorten aantrokken, terwijl de *bunch grass* graslanden vooral werden bezocht door de zwaardere grazer soorten (wildebeest en groter), met name tijdens de eerste maanden na een brand. Op een nog fijnere schaal zijn de meeste graslanden in Hluhluwe-iMfolozi park gekarakteriseerd door een grote ruimtelijke variatie op het *patch* niveau, met snel afwisselende plekken van kort en lang gras binnen enkele vierkante meters. Ik bediscussieer hoe deze heterogeniteit binnen een grasland de mogelijkheden kan vergroten voor grazers om hun voedsel te verdelen en uiteindelijk bijdraagt aan hun coëxistentie (hoofdstuk 5). In een veldexperiment, waar ik variatie in *patch* grootte en graskwaliteit manipuleerde, vond ik dat soorten verschillend selecteerden voor deze eigenschappen van een foerageerplek. Op deze schaal reageren grazers niet alleen op ruimtelijke heterogeniteit maar kunnen ze dit ook zelf vormen. Ik beschrijf en test een schaalafhankelijk mechanisme dat de kort-lang gras dynamiek in graslanden zou kunnen bepalen (hoofdstuk 6). Dit mechanisme is gebaseerd op een interactie van megagrazers, zoals de witte neushoorn, en kleinere grazers, zoals het wrattenzwijn. De megagrazers veroorzaken verstoringen boven een bepaalde ruimtelijke schaal (bv. in de vorm van modderbaden of territoriale concentraties van uitwerpselen), die vervolgens de kleinere grazers aantrekken. De intense, gelokaliseerde begrazing door de kleinere grazers bevordert vervolgens de ontwikkeling van een *grazing lawn*. Preliminair resultaten ondersteunen deze hypothese en de suggestie dat de soortenrijkdom van een grazer gemeenschap een belangrijk aspect is voor het functioneren van een savanne systeem.

In het concluderende hoofdstuk vat ik mijn resultaten samen en bediscussieer ik hoe de verdeling van voedsel tussen grote grazers genest is over verschillende ruimtelijke schalen (hoofdstuk 7). Resultaten van dit proefschrift suggereren dat de verdeling van voedsel niet simpelweg op één ruimtelijke schaal plaatsvindt maar dat grote grazers hun voedsel verdelen in een complex landschap waar een hiërarchische set van factoren de ruimtelijke heterogeniteit van voedselkwaliteit en -kwantiteit bepaalt op verschillende ruimtelijke schalen. Veel studies in het verleden beperkten hun verklaring met betrekking tot de verdeling van voedsel tussen verschillende grazer soorten echter tot één ruimtelijke schaal. De toekomstige uitdaging is dat we studies moeten ontwerpen waar ruimtelijke schaal een integraal onderdeel is van ideeën over hoe grote grazers hun voedsel verdelen. Deze nieuwe studies kunnen wellicht voordeel halen uit nieuwe beschikbare technieken, zoals het meten van vegetatie kwaliteit met behulp van satellietbeelden en het gebruik van satellieten voor het volgen van populaties van verschillende grazer soorten.

Vanuit een praktisch beschermingsperspectief benadrukken de resultaten van dit proefschrift het belang van het in stand houden of bevorderen van ruimtelijke voedsel heterogeniteit op verschillende schalen in het beheer van savanne systemen. Deze resultaten ondersteunen de recente verandering naar een nieuw paradigma in het beheer van graassystemen. Dit zogenoemde *heterogeneity paradigm* zegt dat het beheer grasland heterogeniteit moet bevorderen om biologisch diverse gemeenschappen in deze systemen te behouden. Aan het einde van het proefschrift (hoofdstuk 7) filosofer ik hoe kleinschalige heterogeniteit wellicht een gebrek aan reservaatgrootte kan compenseren, omdat optimale en suboptimale voedselbronnen beschikbaar komen binnen de leefgebieden van sedentaire soorten. Relatief homogene systemen, met slechts grootschalige gradiënten die voedselkwaliteit en kwantiteit beïnvloeden, moeten daarentegen groot genoeg zijn voor soorten om de juiste balans te kunnen vinden tussen optimale en suboptimale voedselbronnen. Als dit verschil inderdaad bestaat, zullen in sommige gebieden grote reservaten inderdaad nodig zijn (b.v. het Serengeti systeem) terwijl in andere gebieden, met een heterogene abiotische achtergrond, kleine reservaten een goed alternatief kunnen bieden voor de bescherming van diverse en abundante grazer gemeenschappen. Dit biedt mogelijkheden voor gebieden waar veel verschillende belanghebbenden concurreren om ruimte, zoals de provincie Kwazulu-Natal in Zuid-Afrika, waar ook Hluhluwe-iMfolozi park is gesitueerd. Met andere woorden de planning van reservaten moet niet alleen gericht zijn op gebieden waar voldoende ruimte is maar ook de potentie voor kleinschalige voedselheterogeniteit zou een belangrijk selectie criterium moeten zijn.

Summary

Large mammalian grazers are among the most conspicuous species groups of the animal kingdom. The richest assemblages of large grazers can be found on the African continent. Diverse large grazer assemblages and the grazing systems they live in have been ascribed great socio-economic as well as ecological value. The impact of wild large grazers on humans has been enormous throughout the evolutionary history of mankind. Domesticated grazers have taken over most of the socio-economic role of their wild counterparts in industrialized societies but in many African countries, where domesticated animals were introduced relatively late, the socio-economic impact of wild ungulates is still strong, forming an important protein source and driving the fast-growing tourism industry. Next to this socio-economic role, the potential influence of large grazers on terrestrial ecosystems can be enormous, from driving large-scale changes in vegetation structure to influencing system nutrient cycling. By shaping the systems they inhabit large grazers influence communities of many other taxa that depend on these systems (from arthropods, to birds and large carnivores). Moreover, an increasing number of studies discuss the importance of grazer species diversity for the functioning of grazing systems as species differ in the way they shape their environment.

Alarming, these diverse grazer communities and their ecological and socio-economic role are increasingly threatened. Free-roaming large grazers have disappeared from large parts of Africa and the remaining areas with high species richness seem to coincide with regions that have the highest human population growth, so the human-wildlife conflict is due to increase. To conserve these diverse assemblages and their functional role we need to understand what factors shape the large grazer communities in time and space. In other words we need to understand how these different large grazer species can locally coexist. Though other aspects such as differences in predation pressure and disease susceptibility have been mentioned, partitioning of the food resource is generally accepted to be the basis of large grazer niche differentiation and ultimately coexistence. In the past several studies have emphasized the importance of body size to explain the separation of feeding niches amongst large African grazers along resource quality and quantity axes, based on the hypothesis that larger grazers can tolerate a lower-quality diet than smaller ones. Prerequisite is that there is sufficient variation in food quality and quantity (i.e. resource heterogeneity) available to large grazer species to be able to coexist. Up to now, in the African context resource heterogeneity has mostly been defined in terms of variation in plant species and in vegetation structure, such as grass height or leaf-stem ratio. Furthermore, several studies argued that different-sized grazers partition resources over time, where species use the same areas and plant species but at different moments in time during large-scale migrations, exploiting different vegetation growth stages that vary in resource quality and quantity. In many areas, however, these large scale

migrations do not (or no longer) occur (such as in many South African reserves). Still these same areas sustain species rich and abundant grazer assemblages without clear evidence of competition for resources. Clear empirical evidence how these species partition their resources is still lacking.

In this thesis I argue that this is partly due to the fact that the spatial dimension has not been well incorporated into our thinking on large grazer resource partitioning. Spatial variation in resource quality and quantity can be defined at different spatial scales, from the feeding patch level to landscape gradients. Past studies have linked spatial variation in resource quality and quantity to single species foraging behavior and some studies have modeled the effect of resource heterogeneity on the stability of grazer population numbers. We, however, lack empirical studies that specifically relate resource heterogeneity to spatial resource partitioning and ultimately coexistence patterns in species rich grazing systems. The aim of this thesis was, therefore, to explore how naturally coexisting large African grazers might spatially partition resources by defining variation in resource quality and quantity at different spatial scales using experimental as well as observational techniques. All studies were carried out in Hluhluwe-iMfolozi Park, a 90.000 ha reserve on the South African east coast, just south of Swaziland and were mainly focused on the 6 commonly occurring large grazer species in the park; impala, warthog, wildebeest, zebra, buffalo and white rhino. In the thesis I start with describing how the body mass of these grazer species influences their distribution over the landscape and how this distribution is linked to landscape variation in habitat type and quality. The larger species were more evenly distributed over the landscape than the smaller species and had a more diverse habitat use, though digestive physiology influenced this relationship. By differently distributing over the landscape, large grazer species might partition their resources at a coarse landscape scale (chapter 3). At a finer scale (hectares) differences in soil type cause spatial variation in grassland types. I describe how grazer species partition these grassland types that differ in resource quality and availability and how fire interacts with grassland type to affect grazer community composition (chapter 4). In general, grazing lawn sites, situated on relatively sandy soils, were nutrient hotspots and attracted all grazer species. On the relatively clayey soils bunch grasslands attracted the larger grazer species (wildebeest and larger), especially in the months after a fire. At an even finer scale (meters), most grassland in Hluhluwe-iMfolozi is characterized by a high spatial heterogeneity at the patch level, with alternating patches of short and tall grass. I showed how this within-grassland heterogeneity might increase opportunities for resource partitioning amongst savanna grazers and ultimately mediate their coexistence (chapter 5). In a field experiment where I manipulated variation in short grass patch size and resource quality I found that species differ in their selection of patch size and quality. Moreover, at this scale grazers do not only respond to heterogeneity, but they can also shape vegetation heterogeneity. I describe and experimentally test a scale-dependent mechanism that might drive short-tall grass

patch dynamics in savanna grasslands (chapter 6). This mechanism is based on an interaction between very large (mega) grazers, such as the white rhino, and smaller grazers. The mega grazers cause disturbances above a certain scale (such as wallows and middens) which attracts smaller grazers. The intense localized grazing of the smaller grazers hence promotes lawn development. These results support the suggestion that the diversity of grazer communities is a significant aspect of savanna ecosystem functioning.

In the concluding chapter I synthesize the results and discuss how resource partitioning among large grazers might be nested across different spatial scales (chapter 7). Results from this thesis suggest that resource partitioning does not simply happen at one spatial scale but that large grazers actually partition a complex resource landscape where a hierarchical set of factors determines the spatial heterogeneity of resource quality and quantity at different spatial scales. However, many studies in the past were actually limited to one spatial scale. Our future challenge is that we need to design studies where we really integrate spatial scale into our thinking about how herbivores partition this complex resource landscape. These new studies might benefit from newly available techniques, such as remote-sensing of vegetation quality and satellite tracking of grazers that allow us to better integrate observed patterns of spatial resource use across spatial scales.

From a practical conservation perspective the results of this study emphasize the need to take spatial resource heterogeneity into account when managing savanna systems. These results support the shift towards a new paradigm in the management of grazing systems. This so-called heterogeneity paradigm states that management should promote grassland heterogeneity to maintain biologically diverse communities in these systems. At the end of the thesis (chapter 7) I philosophize how fine scale heterogeneity might counterbalance a lack of reserve extent, because optimal and suboptimal resources become available in home ranges of sedentary species. In contrast coarse-grained systems, where there are only large-scale gradients that affect resource quality and quantity, have to be sufficiently large for animals to find the right balance of optimal and suboptimal resources. This means that focusing on reserve size would still be necessary in some cases (e.g. Serengeti system) but in places where the abiotic template is heterogeneous small reserves might provide a good alternative supporting diverse and abundant large grazer populations. This offers opportunities for areas where many different stakeholders compete for space, such as the province of Kwazulu-Natal in South Africa where Hluhluwe-iMfolozi Park is situated. In other words next to reserve size, the available scale of heterogeneity of e.g. topography or soil types should be an essential criterion for reserve planning.



Curriculum Vitae

Joris Petrus Gerardus Marinus Cromsigt was born on the 27th of December 1975 in Schijndel, The Netherlands. In 1994 he obtained his high school degree from 'Zelfstandig Gymnasium Beekvliet' in Sint-Michielsgestel. In the same year he started with the biology study at Wageningen Agricultural University, where he received a masters of science degree in September 1999. During his studies he specialized in community and population biology and performed 6-12 month research projects on a range of topics from plant ecology to black rhino population biology. For this last topic he spent some time at the mathematics department of the University of Natal, Pietermaritzburg campus, in the group of Prof. J. Hearne.

After obtaining his MSc degree he worked for half a year for TRAFFIC, at their Brussels office, on a cost-benefit analysis of the role of trophy hunting for biodiversity conservation in central Asia. After this he worked as a private consultant for a period of two years advising on a range of projects for different conservation organizations. Some of the work he did during this period included making a zoological atlas containing the distribution and conservation status of larger herbivore species in Eurasia and analyzing the conflict between EU nature and veterinary policy, both for the Large Herbivore Initiative of WWF International. Furthermore, for the Netherlands Environmental Assessment Agency (RIVM) he contributed to the development of indicators to determine the quality status of Dutch mammal populations. These indicators were developed within the framework of the CBD biodiversity assessments.

After these two years in October 2001 he started to work on the research, presented in this thesis. This project was started at Wageningen University, but was continued at Groningen University at the end of the first year, following the move of the main advisor of the project, Prof. Dr. H. Olff, to this university. Research for this PhD brought him back to South Africa. This time in a field situation in Hluhluwe-iMfolozi Park, for a period of almost 2 years.



List of publications

International journals

Cromsigt, J.P.G.M., J. Hearne, I.M.A. Heitkönig, and H.H.T. Prins. 2002. Using models in the management of Black rhino populations. *Ecological Modelling* **149**: 203-211.

Cromsigt, J.P.G.M., and H. Olf. *In press*. Resource partitioning amongst large savanna grazers mediated by local heterogeneity: an experimental approach. *Ecology*.

Reports

Cromsigt, J.P.G.M. 2000. The large herbivores of the Eurasian continent. A reference guide for the large herbivore initiative (LHI). Large Herbivore Foundation, Voorschoten, The Netherlands.
<http://www.largeherbivore.org/rapportlaatsteversie>

Cromsigt, J.P.G.M., V.A.A. Dijkstra, D. Wansink, and S.E. van Wieren. 2001. Estimating the quality of Dutch mammal populations. Wageningen University, Wageningen, The Netherlands.

Cromsigt, J.P.G.M. 2003. Large herbivores on the move.... A ghost from the past or an indispensable element of the future Eurasian landscape? Large Herbivore Foundation, Voorschoten, The Netherlands.
<http://www.largeherbivore.org/migration.pdf>



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