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# RESOURCE PARTITIONING AMONG SAVANNA GRAZERS MEDIATED BY LOCAL HETEROGENEITY: AN EXPERIMENTAL APPROACH

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

*Key words: African ungulates; body size; community ecology; experimental testing; food quality; large herbivores; resource grain; resource partitioning; savanna grasslands; spatial heterogeneity.*

## Introduction

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

Variation in food quantity has been attributed mostly to variation in the vertical dimension (vegetation height), where different grazers specialize on different heights (Perrin and Brereton-Stiles 1999, Murray and Illius 2000, Farnsworth et al. 2002). However, variation in food quantity also may arise from variation in horizontal dimensions (patch size). Several studies have shown the impact of vegetation patchiness on herbivore foraging behavior (Wilmshurst et al. 1995, Hester et al. 1999, WallisDeVries et al. 1999, Fryxell et al. 2004), but there are few studies examining the effect of such patchiness on local resource partitioning in diverse herbivore assemblages. Resource partitioning along the quality axis has mostly been studied theoretically (Illius and Gordon 1992, Gordon and Illius 1996, Belovsky 1997) with few experimental tests in the field. The above-mentioned studies on food quantity as well as quality

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PLATE 1. This photograph of a warthog family on a grazing lawn in Hluhluwe-iMfolozi Park shows their typical grazing pose—resting on their front knees. Photo credit: Jan Graf.

suggest that savanna herbivores can coexist if spatial heterogeneity in food quality and food quantity is implicitly assumed. However, the difficulty in making this spatial component explicit in analytically tractable models so far has restricted the application and experimental test of these insights to further understand grazer coexistence in savannas.

Using principles of fractal geometry, Ritchie and Olff (1999) incorporated spatial heterogeneity and scale into niche dimensions of local food abundance and food quality to explain the coexistence of different-sized species (see also Olff and Ritchie 2001, Haskell et al. 2002, Ritchie and Olff 2004). They suggested that larger species should perceive and use less spatial detail (coarser grain) of heterogeneously distributed resources. They showed theoretically how these differences in scale of resource perception, combined with variation in patch size and resource quality within patches, can explain the coexistence of different-sized species. Within a size hierarchy, species may use resources exclusively in patches that are of too low resource concentration for the next smaller species, yet are too small for the next larger species. The size ratio (the relative difference between two species that are next to each other in the size hierarchy) and, hence, the number of species, will be set by variation in resource availability and the size of these "exclusive spatial niches," so that populations of all species can be sustained. Based on only the presence of the exclusive spatial niches, this model predicts a minimum number of species that can be sustained without having to understand the outcome of resource competition in the patches that are used jointly by different species. This new explanation for resource partitioning in spatially structured habitats has not yet been tested experimentally.

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

## METHODS

### *Study area*

The study was performed in the Hluhluwe-iMfolozi Park, an 89 665-ha reserve in Kwazulu-Natal, South Africa. Mean annual rainfall varies from 985 mm in high-altitude regions to 650 mm in lower areas, and mainly falls between October and March. Daily maximum temperatures range from 13° to 35°C. The park is inhabited by a complete set of indigenous large herbivores and carnivores (Brooks and MacDonald 1983), including seven species that have grass as a major component of their diet: white rhino (*Ceratotherium simum*), African buffalo (*Syncerus caffer*), plains zebra (*Equus burchelli*), blue wildebeest (*Connochaetes taurinus*), waterbuck (*Kobus ellipsiprymnus*), warthog (*Phacochoerus aethiopicus*, see Plate 1), and impala (*Aepyceros melampus*).

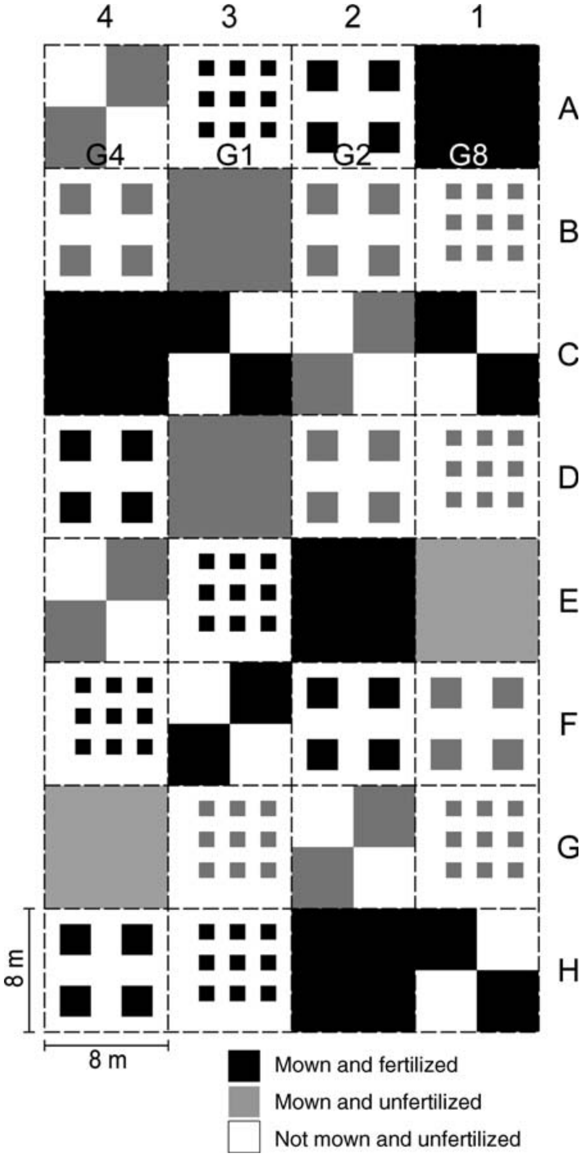

FIG. 1. The experimental layout, consisting of 8 × 8 m treatment plots with a combination of two treatments (grain size and fertilizer application). Manipulated patches are shown in black and gray; the white background represents the untreated matrix of tall grass and shrubs. Half of the plots were fertilized (black), and the other half remained unfertilized (gray). Within each 8 × 8 m plot, we created four different levels of grain of short-grass patches: nine patches of 1 × 1 m (G1), four patches of 2 × 2 m (G2), two patches of 4 × 4 m (G4), and one patch of 8 × 8 m (G8).

### Experimental design

The experiment was set up in the northern part of the reserve, with a yearly average rainfall of ~700–800 mm. Manipulations were performed in an open savanna, dominated by the tall grasses *Eragrostis curvula* and *Panicum maximum*, with bush encroachment of *Dichrostachys cinerea*, *Acacia* spp., and *Gymnosporia senegalensis*. In May 2000 we created an experimental mosaic of different-sized short-grass patches in the tall, woody matrix vegetation using a brush cutter. We subsequently maintained the mosaic with a lawn mower at a height of ~5 cm. After about one year, the grazing pressure kept the grass at approximately this height and, at that point, we stopped mowing.

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

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

The experimental design resulted in eight treatment combinations, with, e.g., G4U being the 4 × 4 m grain, unfertilized patches. Each combination of grain and fertilization was replicated four times. This resulted in 32 8 × 8 m plots that were situated next to each other (Fig. 1) so that we could easily oversee the whole experiment.

### *Effects of treatments on the vegetation*

In July 2002 we took grass samples to determine leaf nitrogen concentrations. We clipped all aboveground grass material within five randomly placed 50 × 50 cm frames in the short-grass subplots of each treatment plot. Before clipping, we estimated the total aerial vegetation percent cover for each frame. Clipped material was dried for 48 h at 70°C. For each sample, we measured the total dry mass (DM), and the DM of leaves, of stems, and of dead organic matter (DOM) as percentage of total DM. Subsequently, we pooled the five dried leaf samples per 8 × 8 m plot and ground and analyzed each pooled sample for total nitrogen content (as a percentage of leaf dry mass) according to the Macro-Kjeldahl method (Donkin et al. 1993). In

September 2002, we recorded grass species composition in five randomly placed 50 × 50 cm frames in the short-grass subplots of each treatment plot. Within each frame, the five dominant grass species were identified. The species were ranked according to their total cover in the frame, receiving a dominance rank from 1 to 5 (in order of increasing cover).

### *Animal visitation*

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

### *Data analysis*

*Effect of treatments on the vegetation.*—Before further analysis, we averaged the dry mass (DM), vegetation percent cover, and species dominance rank values of the five samples that we took per 8 × 8 m treatment plot. We already had one value per treatment plot for percentage of nitrogen, because samples were pooled before N analysis. We tested the effects of the treatments on these variables with two-way ANOVAs followed by Student-Newman-Keuls a posteriori contrasts.

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

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

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

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

*Influence of context of treatment plots on plot selection.*—In the previous analysis, we tested animal preference for resource grain on the 8 × 8 m plot level. The advantage of this analysis was that the grazing time for each grain level was the result of an average of four replicates. This analysis, however, did not account for the different context that surrounded each replicate (see Fig. 1: plot A1 (treatment G8F) was surrounded by matrix, two G2 plots and one G1 plot, whereas plot E2 (also G8F) is surrounded by two G8, one G4, three G2, and two G1 plots and no matrix). We performed another analysis to test whether the context of a treatment plot influenced the selection of that plot. We divided the experiment in a 1 × 1 m grid, and for each grid cell we calculated the proportion of nearby cells with short grass ($p_l$) for different window lengths $l$ around that cell (3, 5, 7, 9, 11, 13, 15, 17, and 19 m). We used this range of window lengths to vary the context of each treatment plot because, beforehand, we did not know the size of the context that would influence the selection of an animal of a certain plot. To calculate an average short-grass context for each 8 × 8 m treatment

TABLE 1. Effect of fertilizer application and grain of short-grass patches on properties of aboveground grass biomass.

| | | | Percentage of total dry mass‡ | | | | | |
|---|---|---|---|---|---|---|---|---|
| Grain | Treatment | DM (g)† | Leaf | Stem | DOM | Leaf N | L:S§ | Cover (%)‖ |
| G1 | fertilized | $3.32^{a}$ | $39^{a}$ | $12^{a}$ | $49^{a}$ | $2.33^{a}$ | $4.43^{a}$ | $15.50^{a}$ |
| G2 | fertilized | $4.13^{ac}$ | $49^{a}$ | $14^{a}$ | $37^{a}$ | $2.78^{a}$ | $4.65^{a}$ | $27.00^{b}$ |
| G4 | fertilized | $4.19^{c}$ | $41^{a}$ | $16^{a}$ | $43^{a}$ | $2.42^{a}$ | $3.25^{a}$ | $38.50^{c}$ |
| G8 | fertilized | $5.04^{c}$ | $43^{a}$ | $18^{a}$ | $39^{a}$ | $2.84^{a}$ | $2.92^{a}$ | $43.50^{c}$ |
| G1 | unfertilized | $4.50^{b}$ | $30^{b}$ | $11^{a}$ | $58^{b}$ | $2.00^{b}$ | $3.58^{a}$ | $16.50^{a}$ |
| G2 | unfertilized | $8.58^{bd}$ | $32^{b}$ | $15^{a}$ | $53^{b}$ | $2.29^{b}$ | $2.45^{a}$ | $27.50^{b}$ |
| G4 | unfertilized | $10.43^{d}$ | $26^{b}$ | $12^{a}$ | $61^{b}$ | $2.06^{b}$ | $2.96^{a}$ | $46.50^{c}$ |
| G8 | unfertilized | $10.43^{d}$ | $29^{b}$ | $10^{a}$ | $61^{b}$ | $2.01^{b}$ | $3.63^{a}$ | $51.75^{c}$ |

*Notes:* Results are based on samples clipped in July 2002, with means ($n = 4$ replicates). Different superscript letters indicate a significant difference within a variable between treatments ($P < 0.05$, Student-Newman-Keuls test after two-way ANOVA). There were no significant interactions between treatments.

† Total aboveground dry mass (g/0.25 $m^2$).

‡ Dry mass of leaves, stems, dead organic material (DOM), and leaf nitrogen content as percentage of total dry mass.

§ Leaf : stem ratio, based on dry mass as a percentage of total dry mass.

‖ Percentage of 0.25 $m^2$ that is covered by vegetation (aerial cover).

plot, we averaged the 64 values of $p_l$ for each 8 × 8 m plot and each window length. Per window length, we sorted the 32 8 × 8 m plots by increasing average $p_l$ value and then aggregated the 32 values into eight classes, calculating an average percentage of grazing time and average $p_l$ per class. Based on these eight averages, we estimated $\gamma$ as the $B$ coefficient from a linear regression of $\log(Q)$ over $\log(p_l)$ and provided 97.5 confidence intervals for $\gamma$ to indicate whether $\gamma$ significantly deviated from 1 ($\alpha = 0.05$). We performed these regressions for all four species for all nine window sizes $l$.

## RESULTS

### *Effect of treatments on the vegetation*

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

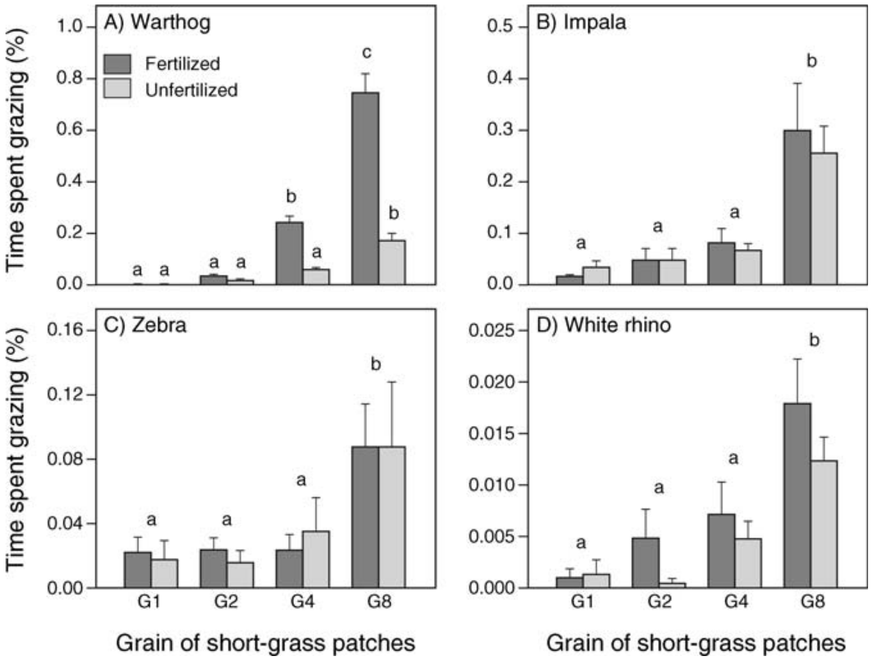

FIG. 2. Percentage of the time spent grazing (mean + SD) by four grazer species, out of the total observation time in the 8 × 8 m plots, for different levels of grain of short-grass patches (see Fig. 1) and fertilizer application treatment. Different letters indicate a significant difference between treatments ($P < 0.05$, Student-Newman-Keuls test after two-way ANOVA).

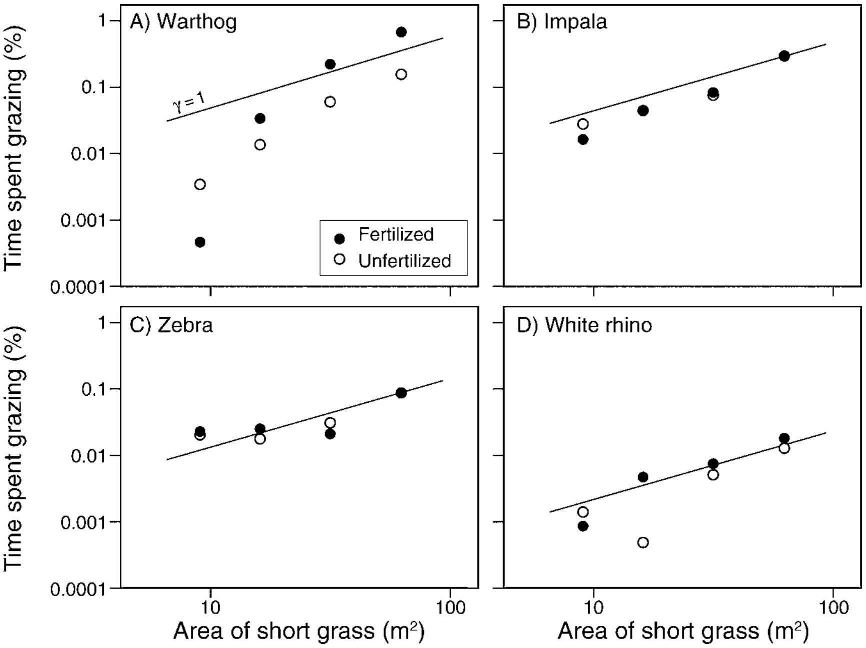

FIG. 3. Scaling of the percentage of time spent grazing with the total area of short grass per treatment plot on a log–log axis. The symbols represent average percentage of the total observation time spent grazing ($n = 4$ replicates) for eight treatment combinations: four levels of total area short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

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

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

### *Animal visitation*

During our observations, the experiment was visited by all grazer species present in the reserve. Buffalo, waterbuck, and wildebeest, however, were observed grazing for only a low number of minutes (>20 minutes). Impala, warthog, white rhino, and zebra were observed grazing long enough to allow statistical analysis: 1798, 2737, 105, and 674 minutes (number of individuals × time observed), respectively.

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

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

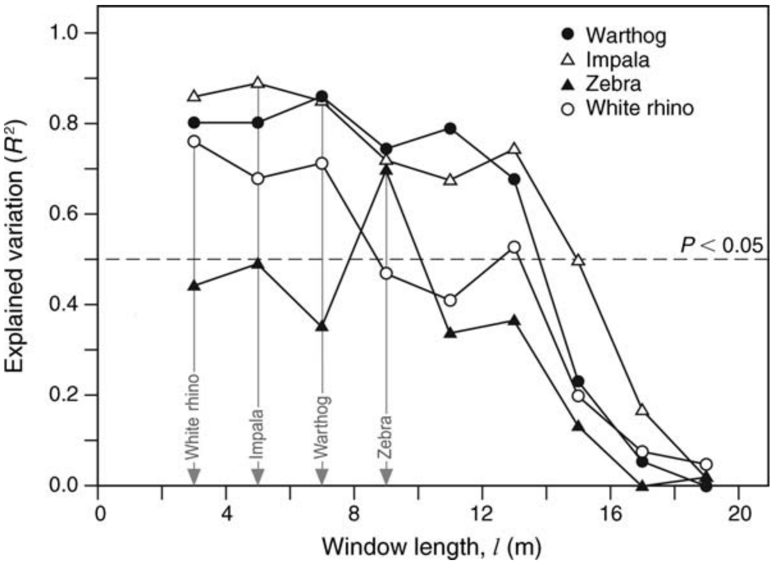

FIG. 4. Explained variation ($R^2$) of regressions of percentage of time spent grazing vs. the proportion of grass in nearby cells around each 1 × 1 m cell, for a range of window sizes (3–19 m), reflecting different scales of resource perception. Results are shown for warthog, impala, zebra, and white rhino. Arrows show the scale of perception (window size) for the four species that had the best-fitting regression. The results of these best fits are as follows (97.5% CI of $\gamma$ in parentheses): for warthog, $\gamma = 3.5$ (1.8–5.1), $R^2 = 0.86$, $P = 0008$; for impala, $\gamma = 2.1$ (1.2–2.9), $R^2 = 0.89$, $P = 0.0004$; for zebra, $\gamma = 1.2$ (0.3–2.2), $R^2 = 0.70$, $P = 0.0094$; for white rhino, $\gamma = 1.8$ (0.6–3.1), $R^2 = 0.76$, $P = 0.0048$.

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

*Influence of context of treatment plots on plot selection.*—The $R^2$ of the regression of log(percentage of time grazed, $Q$) of the four species over log(proportion of short grass in neighboring cells, $p_l$) in a window around a 1 × 1 m cell declined for warthog, impala, and white rhino with increasing window length $l$ (Fig. 4, Appendix). The proportion of short grass in windows of lengths >14 m did not explain further spatial variation in visitation of these three species, because the fit of the regressions steeply declined beyond this scale and they were not significant. With window size <14 m, the fit for warthog and impala did not change much, whereas the fit for white rhino kept improving. For zebra, only the proportion of short grass within window lengths of 9 m contributed significantly to explaining the spatial variation in visitation, and regressions at the other scales were not significant (Fig. 4). Thus the approximate spatial scale at which the percentage of time grazed correlated best with the proportion of grass in neighboring cells declined from zebra, to warthog and impala, to white rhino. The analysis in Fig. 4 also showed that, for the regression with the best fit (with $l = 5$), impala disproportionately avoided finer grain mosaics ($\gamma = 2.1$ with lower confidence interval $>1$).

## DISCUSSION

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

With our experimental study in a natural environment, we chose a site-centered approach to studying resource partitioning among naturally occurring grazers. This time-demanding approach has been used rarely, and has the advantage of direct observation of individuals of species that come from the same local grazer assemblage pool and that can select from the same available resource patches during the same time period. Most studies on resource partitioning among African ungulates have been animal-centered, studying animal food preferences only on those random locations where a certain herbivore is seen (e.g., Underwood 1983, Voeten and Prins 1999). Therefore, they often have the problem that species comparisons must be based on data that originate from different sites and sometimes different time periods, potentially leading to spurious correlations. The few studies that have chosen a site-based experimental approach generally focus on individual foraging behavior instead of community ecology, therefore including only one or two species (e.g., Wilmshurst et al. 1995, Wallis de Vries et al. 1999); thus it is difficult to use their results to discuss general resource partitioning mechanisms.

As mentioned in *Methods*, the amount and the configuration of short-grass patches are confounded factors in our experimental design. One could argue that these factors should be tested separately in a factorial design. However, a design where we would keep the amount constant and vary the configuration has other major disadvantages. In such a design, the spatial extent of the treatment plots would not be the same (e.g., we would get an 8 × 8 m treatment plot for the coarsest grain of one 64-$m^2$ short-grass patch and a 17 × 17 m treatment plot for the finest grain with 64 1-$m^2$ short-grass patches). First, if we used this design, the whole experimental area would become too large to oversee at one glance, making it practically impossible to directly observe animals. Secondly, a significant increase of the total experimental area would have implications for the amount of underlying heterogeneity that is covered by the study; e.g., the natural underlying variation in soil fertility. Different-sized treatment plots would vary in the cover of this underlying heterogeneity, which would be larger in the larger treatment plots than in the smaller plots. Therefore, we chose a design where we kept treatment plot size constant and proportionally increased the total area of short grass between grain levels so that we could use a scaling analysis to test preference for grain level.

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

The fact that we could only analyze the limited number of four species makes it difficult to test the allometric nature of the hypothesis of Ritchie and Olff (1999). This is a generally recognized problem with experimental tests of macroecological theories, where autecological differences overrule the general macroecological patterns in a limited set of species. However, we want to emphasize that four species in itself is not a low number for an experimental test of resource partitioning among savanna ungulates. As discussed earlier, there are almost no site-centered studies that experimentally test resource partitioning patterns including more than one or two species.

Ritchie and Olff (1999) did not explicitly state the relevant range of scales over which they might expect the allometric scaling to occur for different groups of species. Whether the theory holds across other scales is still open to debate and empirical testing. We chose to test their model at the scale of resource patches varying in size from 1 $m^2$ to 64 $m^2$. The allometric relation might, however, become apparent at larger scales, where larger species are more abundant in landscapes that are dominated by large (several hectares), high-quality resource patches (such as postburn grasslands or fertile floodplains), whereas smaller species are more prevalent in landscapes that are characterized by a high proportion of small, high-quality resource patches (e.g., related to trees that locally enhance nutrient availability; Ludwig et al. 2004). On the other hand, the allometric scaling hypothesis might also work on scales smaller than our experiment within a food patch, where smaller grazers select for high-quality parts within a plant and larger grazers forage on the whole plant or a bunch of plants (thereby increasing quantity but decreasing quality of a bite). The original hypothesis, therefore, has to be more widely explored at other scales and locations before we can reject it. The challenge will be to develop appropriate observational and experimental studies at these other scales.

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

Another factor that might confound the testing of the Ritchie and Olff (1999) hypothesis is that not only the partitioning of food resources, but also predation, can shape African ungulate communities (Sinclair 1985). Sinclair et al. (2003) showed that smaller herbivore species in the Serengeti encounter greater predation risk than larger herbivores. Moreover, Sinclair et al. (2003) suggested a threshold body mass of 150 kg marking a transition from predator-limited to resource-limited population dynamics. Following this argument, warthog and impala would be more limited by predation than by food availability. Other studies have suggested that a higher predation risk stimulates animals to choose more open areas (Underwood 1982). This would suggest that our coarser experimental plots could be perceived as safer (with a better view) and may explain the preference of warthog and impala (Figs. 3 and 4) for the coarser resource mosaics. Moreover, note that warthog, the species that avoids finer grain most strongly, is also the smallest of the four species. In contrast with the other three species, it was more difficult for warthog to look over the tall vegetation surrounding the short-grass patches. Thus, warthog might have selected for the coarser grain plots as a predator avoidance strategy.

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

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## APPENDIX

Influence of the short-grass context of treatment plots on plot selection by four savanna grazers using windows with lengths ranging from 3 to 19 m (*Ecological Archives* E087-092-A1).