Competition and coexistence among short-grass grazers in the Hluhluwe-iMfolozi Park, South Africa

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Abstract: Coexistence among grazing ungulates has been related to differences in grass height and grassland types selected, underlain by morphological distinctions. Nevertheless, resource competition may arise when smaller species depress grass height below that suitable for larger species, whereas competition may be counteracted by facilitation when larger species increase the extent of high-quality grassland available. We investigated resource-use overlap between white rhinoceros (*Ceratotherium simum* (Burchell, 1817)), blue wildebeest (*Connochaetes taurinus* (Burchell, 1823)), and Burchell's zebra (*Equus burchelli* (Gray, 1824)) in the Hluhluwe-iMfolozi Park in South Africa. We recorded the grassland type favoured, grass species utilized, grass height grazed, and greenness selected during the dry seasons of 2 years. Blue wildebeest shifted their grazing away from lawn grassland in the drier year, whereas Burchell's zebra favoured lawn grassland only in the relatively wet year. White rhinoceros concentrated their feeding on lawn grassland throughout the dry seasons of both years, and favoured shorter grass than the other two grazers. Species characterizing grazing lawns contributed relatively more to the grass used by white rhinoceros in the drier year. Resource competition was potentially ameliorated by widened availability of lawn grassland promoted by white rhinoceros grazing. This counterbalancing of feeding competition and habitat facilitation enables the coexistence of these grazers despite similar food requirements.

Résumé : On a établi une relation entre la coexistence des ongulés brouteurs et les différences de sélection des tailles des herbes et des types de prairies, qui s'expliquent par des distinctions morphologiques. Néanmoins, il peut y avoir de la compétition pour les ressources lorsque des espèces plus petites réduisent la hauteur des herbes sous le seuil approprié pour les espèces plus grandes, alors que la compétition peut être compensée par la facilitation lorsque les espèces plus grandes favorisent l'augmentation de la disponibilité de prairies de haute qualité. Nous examinons le chevauchement dans l'utilisation des ressources entre le rhinocéros blanc (*Ceratotherium simum* (Burchell, 1817)), le gnou bleu (*Connochaetes taurinus* (Burchell, 1823)) et le zèbre de Burchell (*Equus burchelli* (Gray, 1824)) dans le parc Hluhluwe-iMfolozi en Afrique du Sud. Nous avons noté le type de prairie préféré, les espèces d'herbes utilisées, la taille de l'herbe broutée et le degré de verdure sélectionné durant les saisons sèches pendant deux ans. Durant l'année plus sèche, les gnous bleus abandonnent le broutage dans les prairies à herbes basses, alors que les zèbres de Burchell choisissent les prairies d'herbes basses seulement durant l'année relativement humide. Les rhinocéros blancs concentrent leur alimentation dans les prairies d'herbes basses durant les saisons sèches des deux années et préfèrent des herbes plus courtes que les deux autres brouteurs. Les espèces caractéristiques des pâturages à herbes basses contribuent relativement plus à l'herbe consommée par les rhinocéros blancs durant l'année plus sèche. La compétition pour les ressources est potentiellement améliorée par la disponibilité accrue de la prairie à herbes basses provoquée par le broutage des rhinocéros blancs. Cette compensation entre la compétition alimentaire et la facilitation de l'habitat permet la coexistence de ces brouteurs malgré la similarité de leurs besoins alimentaires.

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Introduction

The extent to which interspecific competition for resources influences the coexistence of large grazing herbivores in African savanna ecosystems remains an unresolved scientific issue (Sinclair and Norton-Griffiths 1982; Sinclair 1985; Prins and Olff 1998; Murray and Illius 2000; Arsenault and Owen-Smith 2002). Some degree of resource partitioning may arise through distinctions in body size, with smaller species requiring more nutritious and hence shorter grass, while larger species are dependent on higher grass biomass and more tolerant of the reduced nutritional value of taller grass (Bell 1971; Jarman 1974; Prins and Olff 1998). Distinctions in relative muzzle width may contribute further to the ability of animals to crop grass differing in height (Owen-Smith 1985; Gordon and Illius 1988; Murray and Brown 1993). Furthermore, nonruminants with hindgut fermentation are better able to process taller and hence more fibrous grass digestively than ruminants of similar size (Bell 1971; Janis 1976). Hence, it has been proposed that spatial heterogeneity

in grassland structure and its modification through grazing could contribute to the coexistence of ungulate species differing in these features in East African communities (McNaughton and Georgiadis 1986; Murray and Illius 1996, 2000).

Nevertheless, it has also been proposed that smaller herbivores can out-compete larger herbivores through their grazing impacts by being able to survive on grass biomass levels too low to support larger species (Clutton-Brock and Harvey 1983; Prins and Olff 1998). On the other hand, larger herbivores are able to exploit a wider range of habitat conditions, and hence through their greater biomass remove much of the grass that would otherwise be exploited by smaller species (chapter 12 in Owen-Smith 2002; Arsenault and Owen-Smith 2002). At the same time, through their grazing impacts the larger species also promote the regrowth of new green shoots that are highly nutritious, thereby perhaps facilitating the co-existence of smaller ungulates (Vesey-FitzGerald 1960; Bell 1970, 1971; McNaughton 1976; Prins and Olff 1998). Longer term facilitation could also arise if these larger grazers transformed much of the grassland structure and composition more conducive to the grazing needs of the smaller species. The counterbalancing of competition and facilitation at different stages of the seasonal cycle could help explain the surprising lack of the population effects expected as a result of competition for overlapping resources among grazing ungulate species (Arsenault and Owen-Smith 2002).

An unusual feature of grazing ungulate assemblages in South Africa, not represented in East Africa (apart from a few introduced animals), is the presence of the white rhinoceros (*Ceratotherium simum* (Burchell, 1817); henceforth white rhinos). This largest extant grazer should be especially tolerant of tall fibrous grass, while also supremely adapted through its wide mouth and lip-plucking grazing technique to crop very short grass (Shrader et al. 2006; Arsenault and Owen-Smith 2008). Hence, white rhinos have the potential to out-compete the two grazers that are most abundant in East African ecosystems: blue wildebeest (*Connochaetes taurinus* (Burchell, 1823); henceforth wildebeest), adapted through their wide incisor breadth to exploit short grass (Murray and Brown 1993), and Burchell's zebra (*Equus burchelli* (Gray, 1824); henceforth zebra), adapted through their rapid digestive passage to handle somewhat tall, relatively fibrous grass (Janis 1976). Nevertheless, through promoting the spread of grazing lawns (Owen-Smith 1988; Waldram et al. 2008), white rhinos also potentially make more high-quality forage available to other ungulates capable of exploiting the relatively short and leafy grasses that become prevalent.

Our study was directed at establishing the extent of overlap in resource use by white rhino, wildebeest, and zebra in the Hluhluwe-iMfolozi Park (HiP), where the white rhino constitute over 40% of the grazer biomass (Owen-Smith 1988), and hence, the implications for coexistence of these three grazers. overlapping quite substantially in their resource dependencies. In this report, we consider not only distinctions in grass height grazed, summarized elsewhere (Arsenault and Owen-Smith 2008), but also differences in relative use of grassland types, grass species, and grass greenness during the course of the dry season, when competition for diminishing food resources is expected to become most intense. So far as we are aware, our study is the first to consider all of these aspects

through the critical dry season period for an African ungulate assemblage.

Our five starting hypotheses were as follows. If competition was of overriding importance, we hypothesized (1) that wildebeest and zebra would become increasingly displaced from their use of lawn grassland as white rhino reduced grass height first below the height favoured by zebra, and at a later stage below the height favoured by wildebeest. If facilitation through structural changes in taller grasslands was important, we hypothesized (2) that zebra and wildebeest would make increasing use of compositionally tall grassland as white rhino depressed the height of tall grasses into the range favoured by zebra and wildebeest over the course of the dry season. We hypothesized furthermore that if facilitation through grass regrowth on grazing lawns was important, (3) the grass grazed by all three grazers on these lawns would be greener than that available in other grassland types early in the dry season, while sufficient soil moisture remained to enabled regrowth. We hypothesized also that because of the oral and digestive distinctions among the three grazers, (4) some partitioning would be apparent in the grass species utilized within grassland types, with zebra concentrating more on taller grass species and wildebeest more on the shortest species, compared with the wide range of species grazed by white rhinos. We hypothesized also that being much larger, white rhinos would select patches at a larger scale so that (5) distinctions between the grassland structure and composition in feeding patches compared with the surrounding grassland matrix should be greater for wildebeest and zebra than for white rhino. To establish the importance of habitat facilitation at a larger scale through persistent transformation of the grassland, we also assessed the relative extent of the lawn grasslands generated primarily through the grazing impacts of white rhinos. By covering all of these aspects, we set out to undertake the most thorough study of the mechanisms potentially underlying coexistence or competitive displacement among the predominant large grazers in African savanna ecosystems.

Materials and methods

Study site

The study was centred on the Mbuzane ranger station in the northwestern region of the iMfolozi section of Hluhluwe-iMfolozi Park, KwaZulu-Natal, South Africa (28°20'S, 31°51'E). The topography is gently undulating and underlain by Ecca shales and sandstones of the Karoo Series plus dolerite intrusions, which produce relatively fertile soils. The predominant tree species in the study area were knobthorn (*Acacia nigrescens* Oliv.) and umbrella thorn (*Acacia tortilis* (Forssk.) Hayne). Mean rainfall recorded at the Mbuzane ranger station was 690 mm (1981–1998). Rainfall was below the mean (545 mm) during the first seasonal cycle (October 1998 – September 1999) and above the mean (791 mm) during the second year of the study (October 1999 – September 2000). Numbers of white rhinos within HiP increased from around 600 animals in 1948 to over 2000 individuals by 1972, subsequently capped at around 1800 by removals. Populations of other major grazing ungulates within the 900 km² extent of HiP at the time of the study were about 25 000 impala (*Aepyceros melampus* (Lichtenstein, 1812)), 3 500 war-

thog (*Phacochoerus africanus* (Gmelin, 1788)), 3 400 zebra, 3 100 wildebeest, 3 200 African buffalo (*Syncerus caffer* (Sparrman, 1779)), and 700 waterbuck (*Kobus ellipsiprymnus* (Ogilby, 1833)) (Waldram et al. 2008). The local abundance of white rhino, wildebeest, and zebra was greater in the study area than elsewhere in the park (Cromsigt et al. 2009).

Data collection

Observations commenced at the start of the dry season in March 1999, and then in May 2000, when dry season conditions became established later in the second year. Observations were terminated in September in both years when early rain brought an end to the dry season. Animals for observation were located by driving a road circuit of 49 km, once early in the morning and once in the late afternoon, during these main feeding periods of the herbivores. When an animal or herd was observed feeding within 200 m of the road, the first animal seen grazing was selected as the focal animal. Its position was identified using nearby landmarks (trees, bushes, rocks, etc.). The herd was then displaced, and a 1 m² quadrat placed over the feeding site. Each grass species present was identified, noting those that had freshly been eaten as indicated by the white appearance of the damaged cuticle. Four grassland types were distinguished, following Downing (1972) and Owen-Smith (1973). Lawn grassland was characterized by stoloniferous or rosette-forming grass species, including Bushveld signal grass (*Urochloa mosambicensis* (Hack.) Dandy), small buffalo grass (*Panicum coloratum* L.), silver finger grass (*Digitaria argyrograpta* (Nees) Stapf), curly-leaved dropseed (*Sporobolus nitens* Stent.), and couch grass (*Cynodon dactylon* (L.) Pers.). Themeda grassland included mainly the medium-tall bunch red grass (*Themeda triandra* Forssk.), narrow-leaved turpentine grass (*Cymbopogon plurinodis* (Stapf) Stapf ex Burtt Davy), and spear grass (*Heteropogon contortus* (L.) P. Beauv. ex Roem. & Schult.). Shade grassland comprised mainly quite tall Guinea grass (*Panicum maximum* Jacq.), broad-leaved panic grass (*Panicum deustum* Thunb.), and needle grass (*Enteropogon monostachyus* (Vahl) K. Schum). Other grassland included mostly pinhole grass (*Bothriochloa insculpta* (Hochst. ex A. Rich.) A. Camus), various species of lovegrass (genus *Eragrostis* Wolf), blue buffalo grass (*Cenchrus ciliaris* L.), and species of bristlegrass (genus *Setaria* P. Beauv.). We also recorded the most prominent grassland type within a 2 m radius of the feeding site, to relate the grass type selected to that generally available in the surrounding foraging area. This was done to accommodate situations where animals were foraging in an area with predominantly tall grass, but chose to feed on the short grass presented on termite mounds or other disturbed sites.

The height of the grass tufts that had been grazed was estimated from measurements of the leaf height of nearby plants of the same species that remained ungrazed, and categorized as ≤5, 6–10, 11–20, and >21 cm. The proportion of green relative to brown leaves was estimated initially using an eight-point scale, then assigned to four categories for analysis: mostly green (75%–100%), mainly green (50%–75%), mainly brown (25%–50%), and mostly brown (0%–25%). The relative use of particular grass species was assessed by dividing the number of quadrats where that species was recorded as eaten by the total number of feeding records across

all grass species, within the temporal periods distinguished. Because *P. coloratum* could not reliably be distinguished from *U. mosambicensis* when plants were cropped very short, records for these two species were amalgamated. The regional availability of grassland types within the study area was recorded by pacing 200 steps perpendicular to the road at every 2 km along the drive circuit, and counting the number of paces where each grassland type occurred within the 200 steps.

Data analysis

For statistical analysis, we distinguished the following 2-month periods within the two dry seasons, based on rainfall patterns: March–April 1999, May–June 1999, July–August 1999, May–June 2000, and July–August 2000. This was done to achieve adequate samples within each period while allowing also for nonlinear trends. Log-linear analysis was undertaken using Statistica 2000 to establish distinctions among herbivore species and periods in proportional use of (*i*) grassland type in the foraging area (four categories), (*ii*) grassland type at the feeding site (four categories), (*iii*) grass height grazed (four categories), and (*iv*) grass greenness present (four categories). The benefit of consistently using categorical factors is that nonlinear relationships are readily accommodated within limited samples.

The relative fit of the full model, including herbivore species, period, and the factors being considered, plus all interactions, was compared against various reduced models using likelihood ratio tests. The statistics presented below represent the reduction in goodness of fit of the model following the removal of the specific factor from the model, based on the χ^2 statistic and significance level of $P < 0.05$. Standardized residuals were used to indicate which particular cell in the contingency table, if any, had contributed mainly to the lack of fit (following Quinn and Keough 2002). Specific comparisons were also made between pairs of herbivore species within each period to establish whether their patterns of selection differed significantly. Because relative use is a derived measure over a block of time, confidence limits are not presented.

Results

Environmental conditions

The estimated proportional area covered by the four grassland types in the study area was lawn grassland (28%), themeda grassland (41%), shade grassland (26%), and other grassland (5%). In 1999, little rain fell after February so that by July the grass was mostly brown (Fig. 1). In 2000, the wet season rainfall was not only greater but extended through April. As a consequence, the grass available within feeding patches was greener in May–June 2000 than it had been during March–April 1999. The three predominant grassland types showed closely similar trends in greenness (Fig. 1). Grass height was consistently much taller in themeda and shade grasslands than in lawn grassland (Fig. 2). Grass height at feeding sites tended to be shorter than in the surrounding foraging areas. The regional grass height in the areas of themeda grassland where the ungulates foraged tended to increase as the dry season advanced in 1999, but not in 2000.

Fig. 1. Trends in rainfall and grass greenness in different grassland types recorded within feeding patches in the study area in western iMfolozi, South Africa.

Fig. 2. Trends in grass height (mean ±SE) recorded in different grassland types in (*a*) foraging areas and (*b*) feeding sites.
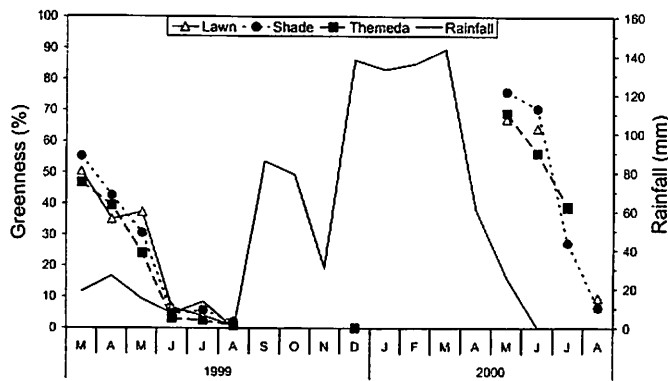
Use of grassland types

Observations amounted to 20–30 feeding records per species per month, leading to the following totals: white rhino (215); zebra (245); wildebeest (246). In the drier year 1999, zebra tended to forage in areas where lawn grassland was less prevalent than in the areas used by the other two grazers but without a seasonal difference in the grassland types selected (Fig. 3*a*). However, seasonal distinctions in the grassland type in the foraging area were evident for both wildebeest ($\chi^2_{[6]} = 17.86$, $P = 0.007$) and white rhino ($\chi^2_{[6]} = 35.24$, $P < 0.001$). Wildebeest occupied other grassland substantially more from May onwards than during March–April. White rhino favoured themeda grassland much more in March–April than later in this dry season. Within feeding sites, wildebeest showed a progressive decrease in their concentration on lawn grassland over the dry season of 1999, as well as increased use of other grassland ($\chi^2_{[6]} = 34.06$, $P < 0.001$) (Fig. 3*b*). White rhino ($\chi^2_{[6]} = 17.85$, $P = 0.007$) and zebra ($\chi^2_{[6]} = 16.98$, $P = 0.009$) tended to graze shade grassland more in July–August than during other periods.

In the wetter year 2000, white rhino, wildebeest, and zebra did not differ significantly in relative prevalence of grassland types in their foraging areas ($\chi^2_{[19]} = 21.75$, $P = 0.297$). All three species concentrated their grazing mostly in places where lawn grassland was prevalent (Fig. 3*a*). However, within feeding sites, distinctions in the grassland type chosen by these three ungulates became evident by July–August ($\chi^2_{[6]} = 16.53$, $P = 0.011$). Zebra tended to make greater use of shade grassland than the other two grazers, and used lawn grassland less than did white rhino (Fig. 3*b*).

Grass height grazed

The three grazers differed significantly in grass height grazed considering all grassland types combined ($\chi^2_{[45]} = 134.49$, $P < 0.001$). White rhino and wildebeest favoured grass ≤5 cm more than zebra in March–April 1999, while in later periods white rhino grazed grass ≤5 cm more commonly than both other grazers (Fig. 4). Zebra tended to graze grass >21 cm more than white rhino in all periods, except March–April 1999.

Wildebeest favoured taller grass than white rhino from May to June ($\chi^2_{[3]} = 12.04$, $P = 0.007$) through July–August 1999 ($\chi^2_{[3]} = 12.13$, $P = 0.007$) (Fig. 4). Zebra favoured taller
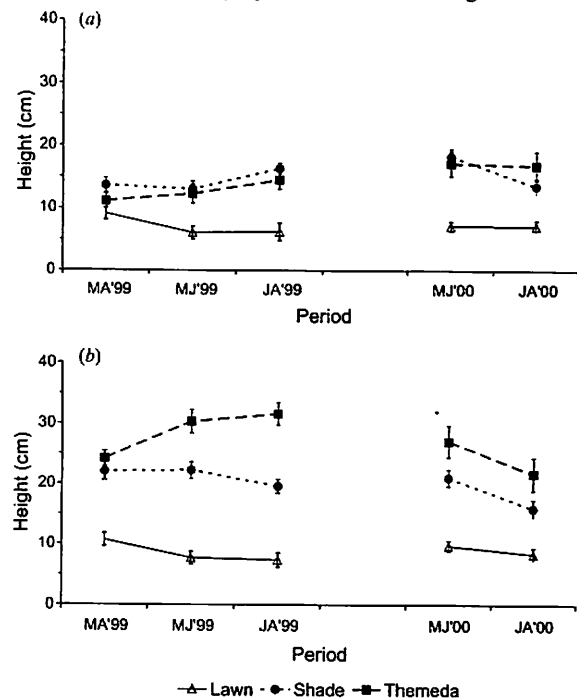
grass than wildebeest in March–April 1999 ($\chi^2_{[3]} = 20.29$, $P < 0.001$), but the difference in grass height chosen for grazing by these two species was not significantly different after May in that year. Significant differences in the grass height grazed among periods were evident in 1999 for wildebeest ($\chi^2_{[6]} = 20.79$, $P = 0.002$) and zebra ($\chi^2_{[6]} = 14.40$, $P = 0.025$) but for not white rhino ($\chi^2_{[6]} = 9.62$, $P = 0.141$). There was a general pattern towards use of taller grass as the 1999 dry season progressed. In 2000, white rhino persistently favoured grass ≤5 cm. Wildebeest showed an increase in their relative use of grass ≤5 cm as the 2000 dry season advanced, whereas zebra shifted towards grass taller than 10 cm (Fig. 4).

Grass greenness

Grass greenness within feeding sites did not differ significantly among the herbivore species. As shown in Fig. 1, shade grassland in the feeding sites was greener in the early dry season than both lawn and themeda grasslands.

Grass species grazed

Relative use of the short grass species characterizing lawn grassland amounted to 50% overall for white rhino and 43% for wildebeest, but made only 27% for zebra (Table 1). Use of lawn grasses by white rhino decreased in the late dry season of 1999, in favour of *P. maximum* growing mainly in shade grassland, whereas wildebeest turned to various other grass species as well as *P. maximum* and *T. triandra* during this period. Zebra grazed mostly *P. maximum* during the latter part of this dry season. In the dry season of 2000, all three grazers made relatively greater use of lawn grasses than in 1999, although zebra used *P. maximum* more than wildebeest and white rhino through July–August. Even though wildebeest and white rhino foraged in places where

Fig. 3. Relative use of grassland types by the four ungulate species in (*a*) foraging areas and (*b*) feeding sites (MA, March–April; MJ, May–June; JA, July–August; 99, year 1999; 00, year 2000).
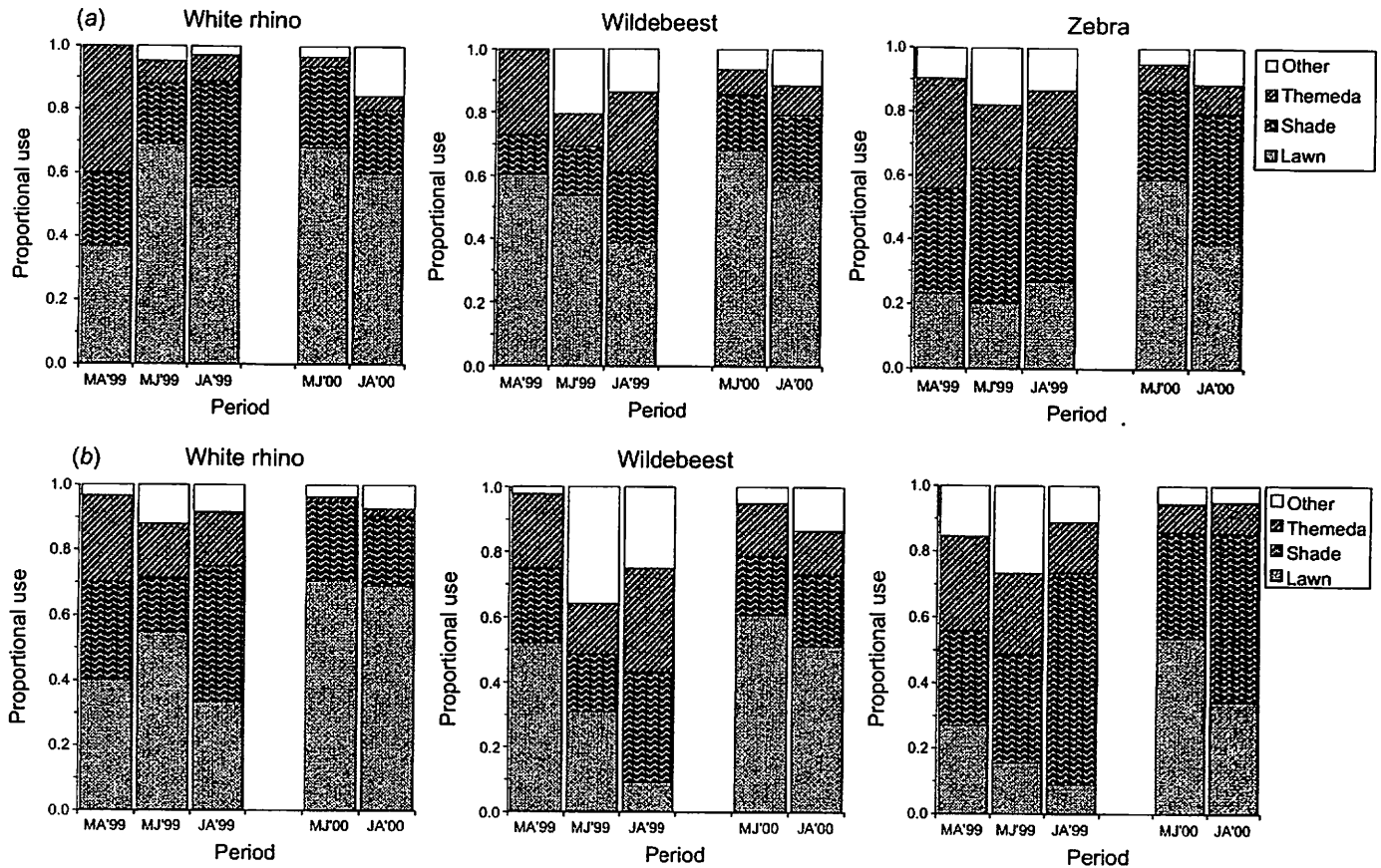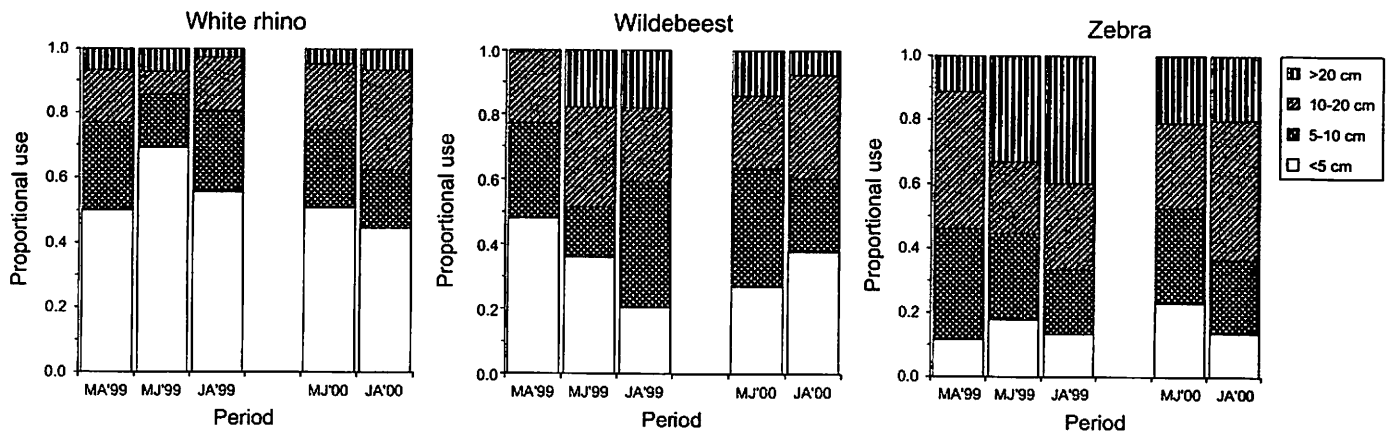

Fig. 4. Relative use of grass height classes by the four ungulate species in feeding sites (MA, March–April; MJ, May–June; JA, July–August; 99, year 1999; 00, year 2000).

lawn grassland was prevalent in a similar proportion of records (Fig. 3*a*), lawn grass species were substantially less important in the food consumed by wildebeest than by white rhino from May through August in 1999 (Table 1). -.

Discussion

White rhino and wildebeest both selected areas where lawn grassland was prevalent to a greater extent than its regional availability during the early stage of the dry season of 1999, and throughout the dry season of 2000 following more plentiful wet season rainfall. Zebra tended to concentrate in lawn

grassland only during the dry season of 2000, following greater wet season rainfall. This indicates that all three grazers favoured the inherently more nutritious grasses of the grazing lawns, provided that adequate forage remained available. Mean grass height in the feeding sites differed little between the 2 years in lawn grassland, but grasses remained considerably greener in the second year. This suggests that the consequently improved nutritional value of lawn grassland in the wetter year was the main influence on this stronger preference.

Zebra were least dependent on grazing lawns and shifted their use towards shade grassland (where *P. maximum* was

Table 1. Relative use of major grass species by the four grazing ungulate species in different seasonal periods in terms of proportional dietary contribution.

Ungulate species	Grassland type	Grass species	1999				2000		Overall mean
			March–April	May–June	July–August	Annual mean	May–June	July–August	
White rhinoceros (*Ceratotherium simum*)	Lawn	*Panicum coloratum + Urochloa mosambicensis*	0.36	0.23	0.15	0.25	0.42	0.47	0.33
		Digitaria argyrograpta	0.03	0.19	0.09	0.10	0.12	0.11	0.11
		Sporobolus nitens	0.03	0.07	0.00	0.03	0.11	0.07	0.06
		Total	0.41	0.51	0.32	0.38	0.66	0.66	0.50
	Shade	*Panicum maximum*	0.26	0.14	0.30	0.23	0.15	0.14	0.20
	Themeda	*Themeda triandra*	0.18	0.14	0.19	0.17	0.02	0.01	0.11
Blue wildebeest (*Connochaetes taurinus*)	Lawn	*Panicum coloratum + U. mosambicensis*	0.28	0.20	0.07	0.18	0.44	0.37	0.27
		Digitaria argyrograpta	0.07	0.11	0.00	0.06	0.10	0.10	0.08
		Sporobolus nitens	0.16	0.07	0.02	0.08	0.07	0.08	0.08
		Total	0.51	0.37	0.09	0.32	0.62	0.55	0.43
	Shade	*Panicum maximum*	0.19	0.13	0.26	0.19	0.14	0.08	0.16
	Themeda	*Themeda triandra*	0.16	0.15	0.26	0.19	0.07	0.12	0.15
	Other	*Setaria* spp. + *Cenchrus ciliaris*	0.00	0.17	0.00	0.06	0.02	0.07	0.05
		Eragrostis superba	0.00	0.07	0.13	0.06	0.03	0.03	0.05
Burchell's zebra (*Equus burchelli*)	Grazing lawn	*Panicum coloratum + U. mosambicensis*	0.26	0.09	0.08	0.14	0.40	0.31	0.23
		Digitaria argyrograpta	0.02	0.00	0.02	0.01	0.06	0.00	0.02
		Sporobolus nitens	0.02	0.00	0.00	0.01	0.06	0.02	0.02
		Total	0.29	0.09	0.10	0.16	0.52	0.33	0.27
	Shade	*Panicum maximum*	0.24	0.27	0.54	0.35	0.22	0.41	0.34
	Themeda	*Themeda triandra*	0.21	0.20	0.14	0.18	0.06	0.06	0.13
	Other	*Setaria* spp.	0.00	0.09	0.02	0.04	0.03	0.04	0.04
		Eragrostis superba	0.02	0.11	0.04	0.06	0.02	0.00	0.04

Note: Species pairs not reliably distinguished in the field have been combined.

prevalent) as the dry season advanced. *Panicum maximum*, although growing fairly tall, is relatively leafy and likely to be of greater nutritional value than most other tall grasses. By switching earlier toward the more nutritious component of the taller grasslands, zebra may have gained some prior advantage over wildebeest and white rhino. Furthermore, because of their greater concentration on taller grassland, the dietary niche of zebra became increasingly separated from that of white rhino as the dry season advanced. Hence, zebra should be less affected by changes in the abundance of white rhino than wildebeest

Rather than concentrating longest on grazing lawns, wildebeest shifted their grazing towards taller grassland types at an earlier stage in the dry seasons of both years than did white rhino. This did not appear to be facilitated by a reduction in height of these taller grasslands, as a result of white rhino grazing, i.e., the mechanism that had been suggested as underlying grazing facilitation by Vesey-FitzGerald (1960). Distinctions in greenness among grassland types also seemed not to be an influence, because the grassland types exhibited closely similar trends in greenness during the dry season. This is contrary to the mechanism identified by McNaughton (1976) for Serengeti grazers. Even when wildebeest foraged in regions where lawn grassland was prevalent, the grasses within the feeding patches they chose had a high predominance of nonlawn species. Wildebeest also made substantial use of other grassland types during the latter part of the dry season, and were recorded feeding quite commonly on sawtooth lovegrass (*Eragrostis superba* Peyr.), which is rated as being of only moderate forage value (van Oudtshoorn 1999). Wildebeest made somewhat less use of *P. maximum* than did zebra. This may have been to avoid the more densely wooded areas (where *P. maximum* was prevalent) on account of the greater cover provided for predators (Talbot and Talbot 1963). However, in 2000 when the lawn grasslands retained substantial green foliage, wildebeest continued feeding predominantly on the lawn grass species throughout the dry season. The seasonal shift by wildebeest towards taller grass seems consistent with competitive displacement, resulting from the progressive depression of forage availability in the lawn grassland by white rhino grazing.

White rhino confirmed their supremacy in ability to exploit very short grass, and during our study period, consistently directed about half of their grazing to areas with grass ≤5 cm. A previous study found that white rhino shifted from 50% occupation of lawn grassland early in the dry season to 70%–90% use of themeda grassland by August (Owen-Smith 1988). Lawn grassland was largely abandoned after its mean grass height was reduced below 5 cm. However, this prior study through 1969–1971 spanned a period when rainfall was below the mean value, and grazing pressure by white rhino was greater because the local white rhino density was about 50% higher than during our more recent study. Under very dry conditions, the competitive impact of white rhino on other grazers could be greater.

Nevertheless, wildebeest and zebra have shown growing populations in HiP, following the cessation of culling after 1983, despite the high white rhino biomass (KZN Wildlife, unpublished records). Off-setting the competitive impact of white rhino is its role in increasing the extent of the lawn grassland (Owen-Smith 1988; Waldram et al. 2008). Lawn

grassland occupied over a quarter of the study area, and other grazers would have experienced greatly reduced availability of these nutritious grasses had white rhinos been less abundant. The population benefit of this grassland transformation for other grazers is likely to be experienced mainly during the wet season when grass regrowth maintains the forage supply (Bonnet et al. 2010), thereby contributing to improved reproductive success. Our findings emphasize how seasonal variation in resource-use patterns needs to be taken into account when assessing competitive relationships among large grazers. They support the proposal by Arsenault and Owen-Smith (2002) that habitat facilitation effective during the wet season can ameliorate resource competition experienced during the dry season. These seasonal trade-offs restrict the population-level consequences of resource-use overlap among grazing ungulates differing in body size and morphological adaptations, and contribute to the coexistence of these species.

Acknowledgements

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