

5 · *Megaherbivores, Competition and Coexistence within the Large Herbivore Guild*

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5.1 Introduction

A special feature of the Hluhluwe-iMfolozi Park (HiP) is the presence of an abundant ‘mega-grazer’ in the form of the white rhinoceros (*Ceratotherium simum*). The study of this species in HiP (Owen-Smith, 1974) led to the identification of common features shared by white rhinos with other extremely large herbivores and hence to the recognition that these ‘megaherbivores’ constitute a distinct life form (Owen-Smith, 1988, 2013a). Defined strictly, the label ‘megaherbivore’ encompasses terrestrial mammals exceeding one metric tonne (i.e. a mega-gram) in adult body mass. The distinguishing ecological and life-history features of these megaherbivores include (1) invulnerability to non-human predation in the adult stage; (2) birth interval exceeding 1 year; (3) maximum rate of population growth typically less than 10% per year; (4) dominance of large herbivore biomass; (5) dietary tolerance for plant structural fibre; and (6) capacity to transform vegetation structure. Extant species manifesting this syndrome include two species of elephant, four rhino species, the hippopotamus, and, marginally, the giraffe (Table 5.1).

While palaeontologists have applied the label ‘megafauna’ to encompass species weighing more than 45 kg (100 pounds), no functional transition is associated with the latter size threshold. Prior to the end of the Pleistocene, megaherbivores were widely represented on all continents (Owen-Smith, 2013a,b). Those formerly present in Europe and northern Asia included the woolly mammoth (*Mammuthus primigenius*)

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Table 5.1. *Extant megaherbivores, their maximum body mass and historical distributions*

Common name	Scientific name	Maximum body mass (kg)		Historical distribution
		Male	Female	
African elephant	<i>Loxodonta africana</i>	6300	3500	Africa-wide
Asian elephant	<i>Elephas maximus</i>	5400	3000	Tropical Asia
White rhinoceros	<i>Ceratotherium simum</i>	2300	1700	Southern and north-eastern Africa
Black rhinoceros	<i>Diceros bicornis</i>	1300	1300	Africa-wide
Indian rhinoceros	<i>Rhinoceros unicornis</i>	2100	1600	Northern India and adjoining countries
Javan rhinoceros	<i>R. sondaicus</i>	1300	1300	Java
Hippopotamus	<i>Hippopotamus amphibius</i>	2000	1850	Africa-wide
Giraffe	<i>Giraffa camelopardalis</i>	1500	1050	Africa-wide

and woolly rhino (*Coelodonta antiquitatus*), both largely grazers, plus two browsing rhinos. North and South America were inhabited by additional species of mammoth, the mastodont, gomphotheres, giant ground sloths, and a hippo-like notoungulate. Australia formerly housed a giant marsupial in the family Diprotodontidae. In Africa, a grazing elephant (*Elephas recki*) and second hippo (*Hippopotamus gorgops*) survived until the mid-late Pleistocene. Cascading extinctions of all megaherbivores and numerous other large mammals followed shortly after the entry of modern humans on all continents outside Africa and tropical Asia during the late Pleistocene (Barnovsky *et al.*, 2004). HiP retains a full suite of extant African megaherbivores, including grazing white rhinos and hippos, mixed-feeding elephants, and browsing black rhinos and giraffes, alongside many less-large grazers and browsers (see Chapter 4).

White rhinos were abundant through much of southern Africa prior to the arrival of Europeans with firearms. Harris (1838) reported seeing 80 white rhinos while hunting near the Magaliesberg in what is now the North-West Province of South Africa, while Smith (1849) encountered over 100 white rhinos during a day's journey with ox-wagons through this region. White rhinos were especially common in Botswana

(Andersson, 1856), and Selous (1899) encountered them throughout Zimbabwe while hunting during the 1870s. The Zambezi river formed the northern limit of their distribution in southern Africa, while the area that became HiP lay at their southern limit. However, white rhinos were absent from the Highveld grassland region. A northern subspecies was present to the west of the Nile river in north-central Africa, but is now extinct in the wild. The absence of white rhinos from apparently suitable habitat in the region between the Zambezi and Nile rivers is evidently of quite recent origin. White rhino remains are abundant in fossil deposits at Olduvai Gorge in Tanzania dated at early to mid Pleistocene. Teeth found on the surface in Tanzania and Kenya plus cave paintings indicate that white rhinos persisted in eastern Africa into the Holocene (Hooijer and Patterson, 1972). It seems likely that the distribution gap is a legacy of past human predation, paralleling the extinctions of megaherbivores elsewhere in the world after the arrival of human hunters with effective spears (Barnovsky and Lindsey, 2010). The fortuitous survival of white rhinos south of the Zambezi river may have been due to the livestock dependency of the Iron Age pastoralists and cultivators who displaced the earlier inhabitants with Stone Age technology (Chapter 1).

White rhinos currently contribute nearly half of the grazing biomass and consume over one-third of all grass eaten by large herbivores in HiP, allowing for effects of body size on metabolic requirements (Owen-Smith, 1988; Waldram *et al.*, 2008). Consequently, the biomass of large herbivores that HiP supports matches that in the Serengeti ecosystem and is twice as great as that in the southern half of Kruger Park (Figure 5.1). Moreover, populations of the largest herbivores in HiP were still growing following the cessation of most culling and the re-introduction of elephants (Chapter 4). Hence it is only in HiP that the full community and ecosystem impacts of a widespread mega-grazer at regional densities approaching three animals/km² and local densities exceeding five animals/km² can be observed. The closest approach to these conditions is in southern Kruger Park where re-introduced white rhinos have reached local densities of up to two animals/km² (Cromsigt and te Beest, 2014).

Coexisting alongside white rhinos in HiP are all of the other large mammalian herbivores that were historically present in the region (Chapter 4), apart from eland (*Taurotragus oryx*; Table 5.2). The continuing growth in the white rhino population, despite annual offtakes under the sink management strategy (Chapter 11), potentially has both beneficial and detrimental consequences for other large herbivores and for the structure and composition of the vegetation. The issues that we will

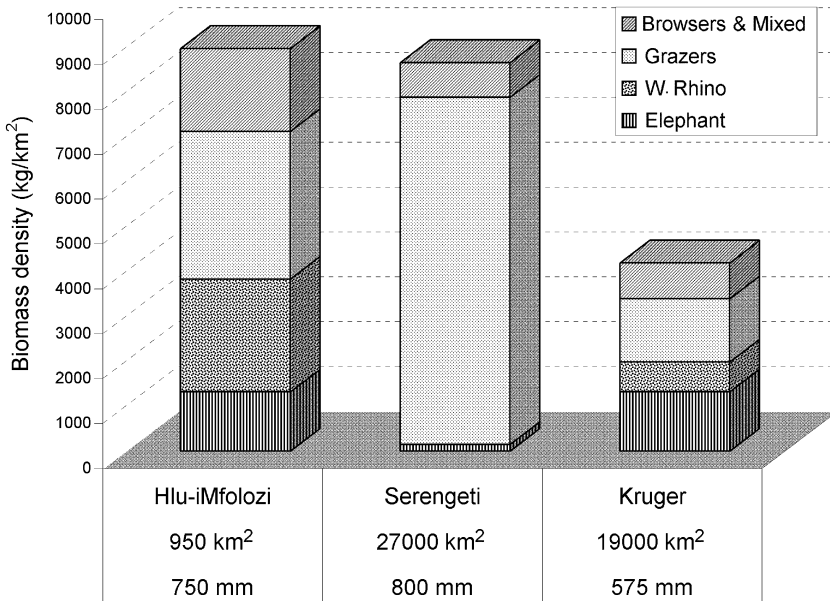


Figure 5.1 Comparative herbivore biomass densities subdivided by dietary categories for Hluhluwe-iMfolozi Park (from mean population totals for 1986–2008 shown in Table 5.2), Serengeti ecosystem (from Mduma and Hopcraft, 1995), and the southern half of Kruger National Park (mean of aerial counts 1980–1993 corrected for undercounting bias except for elephants and rhinos for which most recent estimates were used). Mean body mass is taken to be three-quarters of adult female body mass, from Owen-Smith (1988).

address in this chapter are as follows. (1) How might the growth of the white rhino population ultimately be regulated through its trophic interaction with vegetation, in the absence of predation on adult animals? (2) How do the grazing impacts of white rhinos alter the structure and composition of the herbaceous vegetation layer? (3) What are the consequences of the vegetation transformations wrought by white rhinos for competitive and facilitative interactions within the grazer guild, and hence for the coexistence of other large herbivores?

5.2 Population Regulation in the Absence of Predation

White rhinos do not feature among kills by lions and other large carnivores recorded in HiP (Chapter 12), and there are no records of adult white rhinos being killed by lions or other predators in Kruger National

Table 5.2. *Herbivore populations within the Hluhluwe-iMfolozi Park related to feeding style and body mass (Owen-Smith, 1988; Kingdon and Hoffmann, 2013). Population totals represent the mean over 1986–2008 derived from the density estimates obtained from distance sampling projected over the 950 km² total extent of the park (Chapter 4) except for elephants (2014 total from helicopter counts), and hippo (approximate estimate)*

Common name	Scientific name	Diet category	Maximum body mass (kg)		Population total
			Male	Female	
African elephant	<i>Loxodonta africana</i>	Mixed	8000	4000	698
White rhino	<i>Ceratotherium simum</i>	Grazer	2300	1700	1678
Hippo	<i>Hippopotamus amphibius</i>	Grazer	2065	1850	30
Black rhino	<i>Diceros bicornis</i>	Browser	1300	1200	230
Giraffe	<i>Giraffa camelopardalis</i>	Browser	1500	1050	600
African buffalo	<i>Syncerus caffer</i>	Grazer	860	640	4193
Plain's zebra	<i>Equus quagga</i>	Grazer	375	385	2979
Greater kudu	<i>Tragelaphus strepsiceros</i>	Browser	345	210	1186
Waterbuck	<i>Kobus ellipsiprymnus</i>	Grazer	290	210	510
Blue wildebeest	<i>Connochaetes taurinus</i>	Grazer	280	230	2476
Nyala	<i>Tragelaphus angasi</i>	Mixed	140	80	6086
Warthog	<i>Phacochoerus africanus</i>	Grazer	105	75	2462
Common reedbuck	<i>Redunca arundinum</i>	Grazer	105	65	35
Bushpig	<i>Potamochoerus porcus</i>	Omnivore	80	55	102
Impala	<i>Aepyceros melampus</i>	Mixed	75	55	13,288
Bushbuck	<i>Tragelaphus scriptus</i>	Browser	55	40	66
Mountain reedbuck	<i>Redunca fulvorufula</i>	Grazer	40	35	29
Grey duiker	<i>Sylvicapra grimmia</i>	Browser	21	25	645
Red duiker	<i>Cephalophus natalensis</i>	Browser	17	18	289
Steenbok	<i>Raphicerus campestris</i>	Browser	14	15	51
Blue duiker	<i>Cephalophus monticola</i>	Browser	4	5	6

Park, although immature white rhinos sometimes fall victim (Pienaar, 1969; Owen-Smith and Mills, 2008). When disturbed, subadult white rhinos adopt a defensive formation standing with rumps pressed together, facing outwards. This response seems designed to ward off potential predators. Furthermore, white rhino mothers with small calves stand protectively over the infant, rather than running off. White rhinos flee only in response to the threat posed by human intruders. While young white rhinos are seldom attacked by lions or spotted hyenas in HiP, there are records of black rhino calves being killed by spotted hyenas in HiP (Hitchins and Anderson, 1983) and by lions elsewhere (Brain *et al.*, 1999). The hippos killed by lions in Kruger Park are mostly young animals. In Botswana and Zimbabwe, young elephants as large as half-grown may be killed by lions hunting in large prides (Joubert, 2006; Loveridge *et al.*, 2006).

With little impact from predation, white rhino populations must ultimately be regulated either through effects of their feeding on food resources or via social mechanisms. While territoriality could be an effective regulating mechanism for some species (e.g. for most carnivores), territorial exclusion affects only the distribution of male white rhinos, and hence cannot control overall population growth (Owen-Smith, 1975). Accordingly, population regulation must eventually come about through the effects of malnutrition on life-history features, specifically the birth interval, age at first reproduction, and postnatal survival of offspring, as documented for elephants in East Africa (Laws *et al.*, 1975) and black rhinos in HiP (Hitchins and Anderson, 1983).

By 1970, the total white rhino population within the 950 km² extent of HiP had exceeded 2000 animals, with local densities of over five rhinos/km² attained in sections of western Mfolozi. Despite the grassland transformation that was occurring, the population was still increasing at over 9% per year, close to its maximum potential rate (Owen-Smith, 1988). This growth rate was generated by a mean birth interval of around 2.5 years, age at first parturition of 6–7 years, and offspring survival rate > 90% over the first year. Adult mortality rates were estimated to be only 1.5% per year among females and 3.5% among males, from accidents or injuries incurred in fights. Few adults died of old age, because such animals would have been born 40 years earlier when the population was very small. There were no signs that the physical well-being of white rhinos was being affected by the density levels attained, even in low rainfall years. Nevertheless, erosion gullies were expanding and soils bared of much grass cover were washing down-slope, threatening the sustainability of the resource base. The concern of

park managers was that a rhino 'slum' would develop, with starving white rhinos existing within a degraded habitat. Such a situation could be disastrous for other species, and hence for the wider aims of biodiversity conservation.

Somehow the growing white rhino population needed to be transformed into an effectively stable one. How might this come about solely through the interaction with food resources? With inter-birth intervals spanning multiple years, the critical reproductive stages (gestation, birth, and weaning) are less responsive to annual variation in food availability than for annually breeding ungulates. The effects of malnutrition on reproductive rates become expressed in the population growth rate only a generation later, due to the continuing recruitment of animals already born into the adult segment. Because of this delay, habitat deterioration could pass critical thresholds before the growth of the white rhino population was halted. The only mechanism capable of counteracting the growth of megaherbivore populations sufficiently promptly is dispersal, i.e. animals moving from where they were born to settle elsewhere. This implies a source-sink structure, with animals moving out from the crowded core region into less-favourable localities where the population might not persist in the absence of immigration.

There was evidence that dispersal was indeed taking place before the boundary fence enclosing the game reserve was completed, undertaken mainly by subadult white rhinos of both sexes plus some adult males (Owen-Smith, 1988). Compared with the overall population structure, the high-density core showed an excess of adult females with calves, and peripheral regions a preponderance of adult males plus subadults. The rate of local density increase in the most densely populated region was only half of the overall rate. Dispersal rates estimated from changes in the population composition in core and border regions between successive censuses, taking into account animals removed, indicated that about 7.5% of subadults moved out of the core region per year. A simulation model showed that this rate of dispersal could potentially prevent the population from exceeding the threshold density leading to progressively diminishing food resources. However, with HiP becoming completely fenced, how could such dispersal take place?

The proposed resolution of this management dilemma was the establishment of dispersal sinks within the boundaries of HiP (Owen-Smith, 1974, 1981, 1983). To maintain these low-density regions, or 'vacuum zones', rhinos settling within them would need to be captured and relocated elsewhere. Rather than imposing some arbitrary ceiling on the white rhino population through widespread removals, the animals

themselves would indicate when resources became effectively limiting by moving from the core area into sink zones. Furthermore, the sink zones would provide habitat refuges for plant and animal species adversely affected by the grassland transformations brought about by white rhinos in the core region. This management strategy pioneering the application of concepts of source–sink population dynamics was eventually adopted, and its implementation and outcomes are described in Chapter 11.

The key finding here was the importance of dispersal for the regulation of megaherbivore populations in response to diminishing food availability, because demographic changes would be too slow-acting to avoid potential over-shoot of the ultimate carrying capacity (Laws, 1969; Caughley, 1976). Comprehensive population surveys covering HiP enabled dispersal rates by white rhinos to be measured and incorporated into models of coupled herbivore–plant dynamics (Owen-Smith, 1988). However, the uncertainty was what level of grazing would lead to progressive vegetation deterioration and hence to the irruptions and crashes to which herbivore populations are prone in the absence of predation and when opportunities for dispersal are precluded (Caughley, 1976; Gross *et al.*, 2010). Nevertheless, the implementation of dispersal sink concepts has alleviated concerns about overgrazing up to the present time (Chapter 11).

5.3 Diet Selection and Grassland Impacts of a Mega-Grazer

Field observations of the food consumed by white rhinos in HiP confirmed that they are strictly grazers. Forbs (non-grassy herbs) contributed no more than 1% to the material ingested (Owen-Smith, 1988; Shrader *et al.*, 2006), and no browsing on woody plants was observed. Using their broad mouths (20 cm in diameter) and lip-plucking technique, white rhinos are able to crop grass as low as 25 mm above soil level. Their cropping action promotes grass species that are low-growing and spread via stolons or rhizomes, forming grazing lawns (McNaughton, 1984; Waldram *et al.*, 2008; Hempson *et al.*, 2015; Figures 5.2 and 5.3). Due to their low stature, lawn grasses have less structural fibre than taller grasses, and hence constitute the most nutritious forage on offer to grazers. A broad mouth enables white rhinos to obtain an adequate rate of intake from grass swards that would otherwise be too short to meet their quantitative food intake requirements (Owen-Smith, 1988; Shrader *et al.*, 2006). Hippos with even wider mouths than white rhinos



Figure 5.2 White rhino male grazing short grasses (photo: Norman Owen-Smith).



Figure 5.3 Extensive grazing lawn promoted by white rhino grazing in western Mfolozi during 1970 (photo: Norman Owen-Smith).

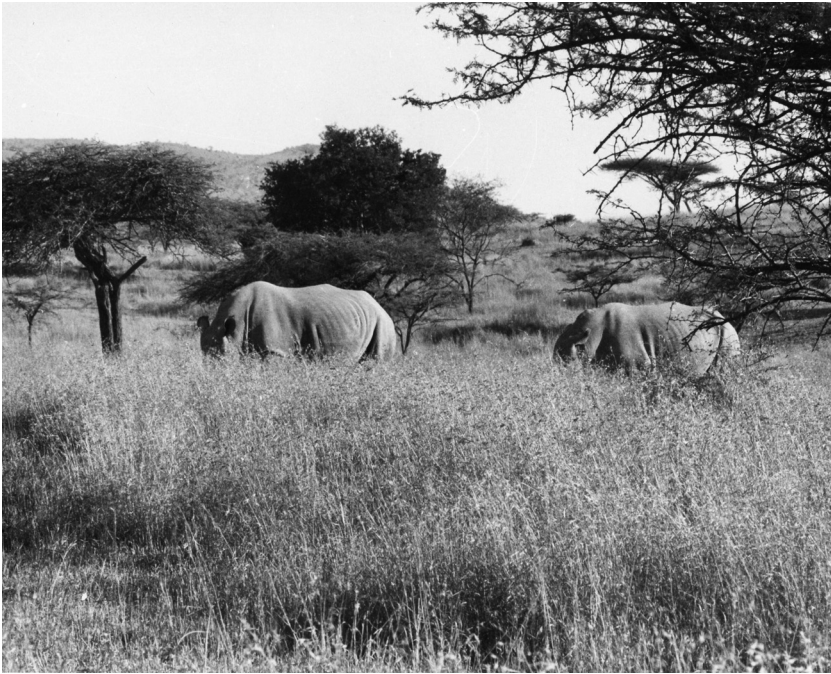


Figure 5.4 White rhinos grazing in tall grassland dominated by red grass during the dry season, but seeking local patches of short grass associated with termite mounds (photo: Norman Owen-Smith).

similarly cultivate the formation of grazing lawns (Olivier and Laurie, 1974). However, the grazing impacts of hippos are confined to the vicinity of the rivers and lakes where they seek refuge during the day, whereas those of white rhinos are spread more broadly across regional landscapes.

White rhinos concentrate their grazing on the lawn grasslands as long as these retain sufficient forage (Shrader *et al.*, 2006). Once lawn grasses have become reduced to stubble, white rhinos shift their grazing to stands of taller grass (Owen-Smith, 1988). Initially they seek guinea grass (*Panicum maximum*), the most nutritious of the bunch grasses, which typically grows under tree canopies. At a later stage in the dry season, they mow down the tall grasslands dominated primarily by red grass (*Themeda triandra*; Figure 5.4). After stands of red grass become closely cropped, white rhinos move onto hill slopes where tall grass remains available (Figure 5.5; Owen-Smith, 1988). Accordingly, different grassland components support white rhinos through different stages of the seasonal cycle (Owen-Smith, 1988). The functional distinctions are between (1)

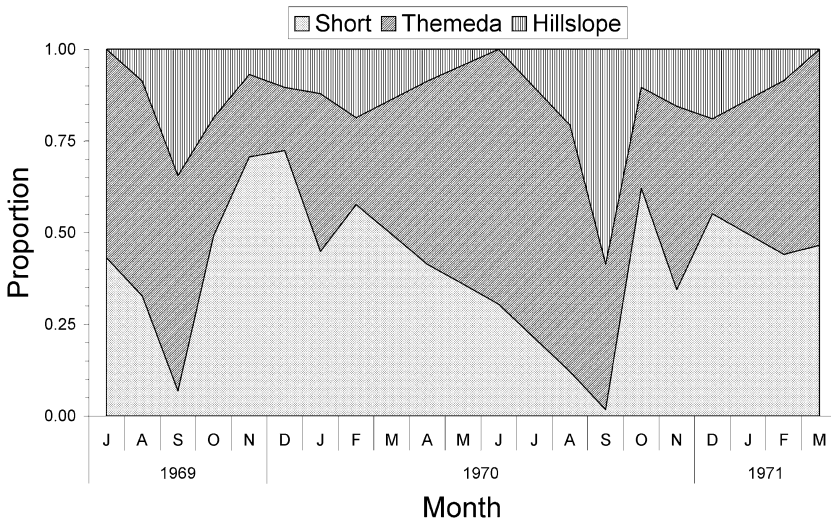


Figure 5.5 Proportional use of grassland types by white rhinos in western Mfolozi during 1969–1971. Short grassland is represented by grazing lawns, Themeda grassland is the medium–tall grassland dominated by *Themeda triandra* (red grass) on relatively flat terrain, and hillslope grassland is constituted by predominantly *T. triandra* growing on steeper slopes (adapted from figure 3.7 in Owen-Smith, 1988).

short-grass lawns providing staple high-quality forage; (2) relatively nutritious bunch grasses grazed during the course of the dry season, providing reserve forage; and (3) less-nutritious or less-accessible grasslands, serving to buffer starvation rates after other sources of forage have mostly been consumed.

It has been inferred that greater size and consequently prolonged digestive retention enables larger herbivores to digest forage more completely than smaller herbivores, and that ruminants lose their advantage in digestive efficiency over hindgut fermenters once a body mass of 1000 kg is surpassed (Demment and Van Soest, 1985). However, there is a limit to how effectively grass tissues can be digested, dependent on the fraction constituted by structural cellulose (Muller *et al.*, 2013). White rhinos and other megaherbivores with hindgut fermentation can tolerate a greater dilution of digestible material by structural fibre than can medium–large ruminants because of their very large size coupled with hindgut fermentation (Clauss *et al.*, 2003). The downside of faster digestive passage is greater sodium losses through the digestive tract, increasing dietary

requirements for sodium (demonstrated for black rhinos by Clauss *et al.*, 2007). Lawn grasses favoured by white rhinos have higher concentrations of sodium as well as other nutrients than surrounding bunch grasses (Stock *et al.*, 2010). The high sodium requirement could help explain why white rhinos were historically absent from cooler Highveld grasslands where there is less evaporation and hence little concentration of sodium in the topsoil.

Through their grazing, white rhinos promote a mosaic of lawn grasslands amidst the prevalent bunch grasslands (Owen-Smith, 1988; Waldram *et al.*, 2008). During the early 2000s, grazing lawns covered about 13% of HiP overall, but extended over as much as a quarter of the landscape in western Mfolozi where the highest white rhino densities occurred (Cromsigt, 2006; Arsenault and Owen-Smith, 2011). The grazing down of bunch grasslands and establishment of grazing lawns restricts the spread of fires (Owen-Smith, 1988; Waldram *et al.*, 2008). Grazing by white rhinos also counteracts the accumulation of dead or moribund grass tissues that builds up in the absence of fire or grazing. It might be expected that woody plants would invade following the suppression of fires in grazing lawns, but this seems not to happen. Conditions might be too dry for seedling establishment, and woody seedlings that emerge are exposed to browsers like impalas. White rhinos also damage woody plants by horning small bushes and then dragging their feet over them during their urine marking ceremonies (Owen-Smith, 1975).

Hence, while elephants radically transform the tree layer (Laws, 1970), white rhinos alter the structure, composition, and functioning of the herbaceous layer, along with other major drivers of savanna vegetation dynamics (Waldram *et al.*, 2008; see Chapter 6). The grassland mosaic that white rhinos promote modifies the landscape heterogeneity underlain by geology and soils (Chapter 2). This in turn influences food availability for other grazers, with possibly both positive (facilitative) and negative (competitive) outcomes for these species.

5.4 Resource Partitioning, Competition, and Facilitation within the Grazer Guild

Over evolutionary time frames, competitive relationships among species sharing the same basic food resource should theoretically lead to niche partitioning. For mammalian herbivores, a major influence on resource partitioning comes from physiological mechanisms dependent on body size (Prins and Olff, 1998). Metabolic requirements for energy and

nutrients increase allometrically with body mass with a power coefficient of approximately 0.75, meaning that larger animals have lower specific requirements per unit of body mass. On the other hand, the volume capacity of the gut to accommodate food varies in direct relation to body mass. This means that larger animals can either eat relatively less food per day per kg of body mass, or consume a similar amount of food but of a lower nutritional content than smaller animals (Bell, 1971; Jarman, 1974). For mammalian herbivores, the nutritional value of the forage consumed is diluted by the structural fibre content of plant tissues that is chemically ligno-cellulose. Larger herbivores can thus tolerate a greater dietary fibre content than can smaller herbivores. This does not mean that they should preferentially seek a high-fibre diet, but rather that during stressful times they can survive on fibrous plant tissues that provide inadequate nutrition for smaller herbivores. Accordingly, smaller species should specialize on the best quality food resources, while larger species should exploit a wider range in quality (Jarman, 1974). This implies that the smallest grazers should selectively graze nutritious short grasses or especially nutritious grass parts, while larger species spread their grazing over taller more fibrous grasses. Differences in digestive system between ruminants and non-ruminants modify relative efficiency in exploiting food quality, because hindgut fermenters have a faster digestive turnover and hence can tolerate higher fibre contents than can ruminants (Janis, 1976).

Observations made in HiP showed that distinctions in muzzle width relative to body mass modify the effects of body size differences (Arsenault and Owen-Smith, 2008). Despite being the largest grazer, white rhinos concentrate on the shortest grass, while considerably smaller impalas graze grass heights intermediate between those cropped by wildebeest and zebra. This is because the wide mouth of white rhinos, coupled with their lip-plucking technique, enables these animals to exploit short grass very effectively (Owen-Smith, 1988). On the other hand, impalas with relatively narrow muzzles can pluck the most nutritious leaves from within both short and comparatively tall-grass swards.

The expected gradient in grass height and quality in the forage consumed by herbivores of different body size was found in HiP, over the size range from warthog through impala and zebra to buffalo (Kleynhans *et al.*, 2011; Figure 5.6). However, wildebeest exploited shorter grass than impala, enabled by their relatively broad muzzles (Arsenault and Owen-Smith, 2008), and during the wet season white rhinos selected grass as short as grazed by warthogs (Cromsigt, 2006). During the dry season

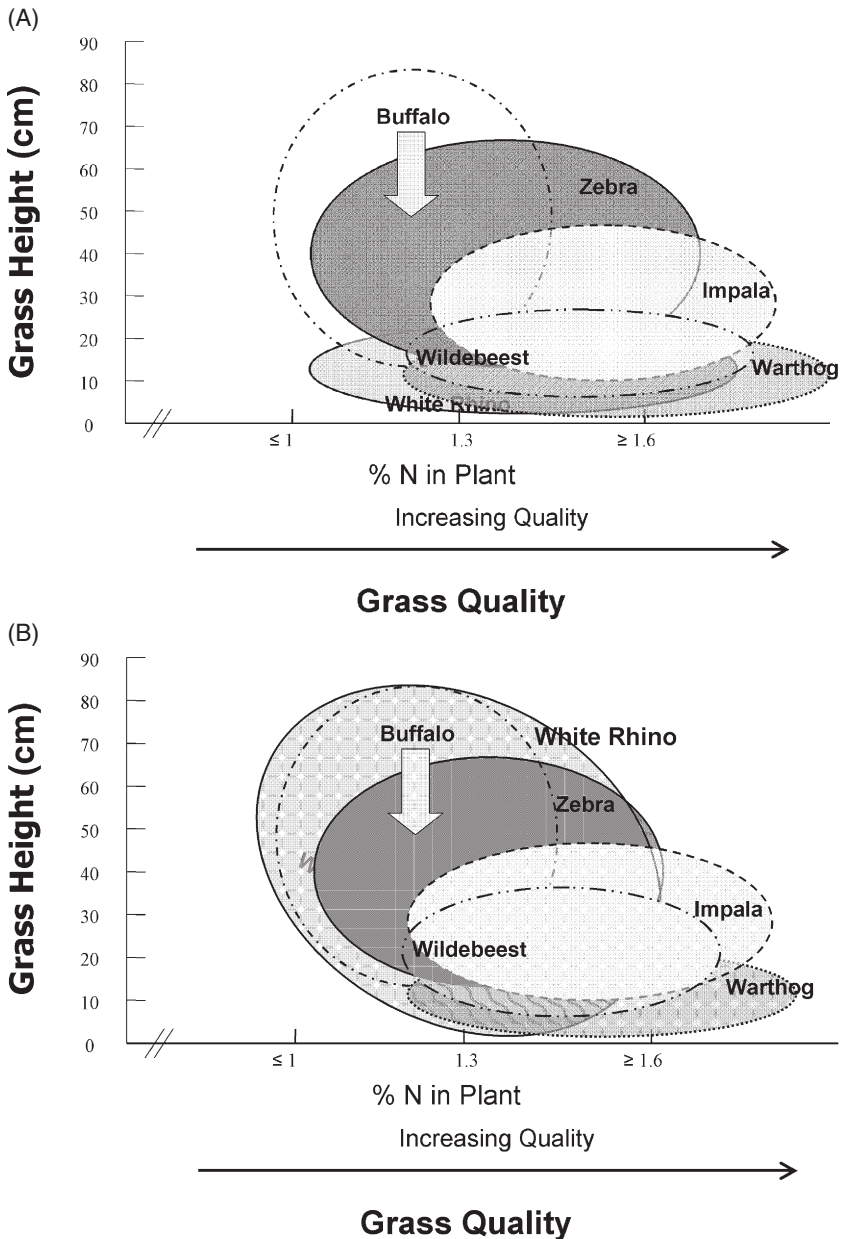


Figure 5.6 Resource partitioning among large grazers in Hluhluwe-iMfolozi expressed in axes of forage quality and quantity (adapted from Kleynhans *et al.*, 2011). (A) Wet season pattern, indicating how white rhinos select short grass of higher quality than expected for their size. (B) Dry season pattern, showing how white rhinos extend their food selection to encompass taller grass of lower quality.

when white rhinos turned their attention towards taller grass, they overlapped with other grazers like buffalo and zebra in the grass height and quality that they utilized. There was also much overlap between white rhinos and other grazers in grass species consumed (Arsenault and Owen-Smith, 2011; Kleynhans *et al.*, 2011). White rhinos exploited mainly lawn grasses, plus guinea grass growing under tree canopies during the wet season, shifting to red grass during the course of the dry season. Warthogs concentrated mostly on lawn grasses throughout the year, but dug up underground grass parts during the dry season. Wildebeests and impalas utilized mainly lawn grasses during the wet season, but reduced their use of these short grasses during the dry season. Wildebeests then exploited a variety of grass species while impalas shifted towards browse. Zebras concentrated especially on guinea grass throughout the year, while buffalos favoured red grass particularly during the dry season.

Resource partitioning could also be effective spatially, with smaller herbivores able to exploit more localized patches of favourable vegetation than larger species (Ritchie and Olff, 1999). This was investigated experimentally within HiP by creating short-grass patches at different size scales within plots that were either fertilized to increase forage quality or left unfertilized (Cromsigt and Olff, 2006). The set-up mimicked the tall–short grass mosaics generated by rhino foraging. As expected, the smallest species, warthog and impala, strongly selected for fertilized plots. However, contrary to expectations, warthog and impala avoided plots with the finest grain. The larger species, white rhino and zebra, appeared unselective and also used the small short-grass plots.

When white rhinos extend their habitat use into predominantly tall-grass areas during the dry season, they initially concentrate their grazing on termite mounds only a few square metres in extent (Owen-Smith, 1988). These local patches may be avoided by small grazers because of the perceived predation risk associated with the surrounding tall grass and shrub cover. Habitat heterogeneity at larger spatial scales could also facilitate spatial separation among grazers. Dung accumulations indicated that larger ruminants were more evenly distributed than smaller ones through occupying a wider diversity of habitats, including those of lower quality (Cromsigt *et al.*, 2009). Furthermore, non-ruminants were more evenly distributed than ruminants of similar size. Hence, size-dependent habitat partitioning among these grazers seemed consistent with habitat relationships among browsers in Kruger Park described by du Toit and Owen-Smith (1989).

The high degree of overlap among grazers in grass height, quality, species, and habitats utilized observed in HiP suggests that there should be considerable potential for competitive displacements. Because of their efficiency in exploiting very short grass, white rhinos should outcompete smaller grazers, like wildebeest and zebra, through depleting stands of the best-quality short grasses. On the other hand, white rhinos promote the spatial spread of nutritious short grasses for lesser herbivores by expanding the grazing lawns and through mowing down fibrous tall grasses. It thus seems surprising that the growing population of white rhinos in HiP (Chapter 11) has apparently had such little influence on the abundance of most other grazers (Chapter 4).

To explain this enigma, Arsenault and Owen-Smith (2002, 2011) suggested that the competitive and facilitative effects of grazing by white rhinos on food availability for other herbivores compensate seasonally. Evidence of competitive displacement is provided by the shift by wildebeest from lawn grasslands towards taller bunch grasslands earlier in the dry season than shown by white rhino, and by observations that zebra made much use of lawn grasslands only in the wetter of 2 years when grasses remained greener into the dry season. However, the extent of the short grass available to other grazers is increased by the grassland impacts of white rhinos, not only through the expansion of grazing lawns, but also by the reduction in height of bunch grasslands during the dry season. The latter impact also restricts the build up of dead grass tissues that otherwise occurs in the absence of fire. As a result, other grazers benefit through having access to better-quality forage during the wet season and early dry season, at the cost of less forage remaining to support them later in the dry season. Hence the overall outcome for the abundance of other grazers could be negligible.

5.5 Resource Partitioning among Browsers

Comparisons have been made between the effects of mega-grazers like white rhinos in cultivating grazing lawns, and those of mega-browsers, like elephants, black rhinos, and giraffe, in promoting the development of browsing 'lawns' (Fornara and du Toit, 2007; Cromsigt and Kuijper, 2011) or 'hedgcs' (du Toit and Olff, 2014). Pruning of the twigs and branches of tree saplings can maintain these plants within the height range where they are readily accessible to large browsers, while also retaining foliage within the height range of smaller browsers (Makhabu *et al.*, 2006). In this way, mega-browsers like elephants can facilitate food access by other

browsers. This depends on the extent to which the plant species favoured by these herbivores overlap, and also on habitat choices. Resource partitioning may also occur through distinctions in height ranges of trees and shrubs browsed, dependent on the size of the browser (du Toit, 1990).

However, the widened use of habitat types with increasing body size found by du Toit and Owen-Smith (1989) in Kruger Park was not evident among the five browsers compared in HiP by O’Kane *et al.* (2011, 2013). The two smallest species, impala and nyala, overlapped most broadly with elephants in habitat use. Partial separation in tree heights exploited was evident between the two tallest browsers, represented by elephant and giraffe, and the two smallest browsers, with kudu intermediate. At plant species level, eight woody species were common to the core diets of all five browsers, with the dietary species range being narrowest for giraffe and widest for elephant.

Investigations on how food availability for smaller browsers is affected by the browsing impacts of the three mega-browsers have yet to be undertaken. An important issue still unresolved is whether increasing numbers of elephants (Chapter 14) will reduce or enhance food availability for black rhinos.

5.6 Consequences of the Biomass Dominance by White Rhinos

The high biomass density attained by white rhinos within HiP contributes largely to an overall large herbivore biomass matching that in the Serengeti region of Tanzania, where migratory wildebeest predominate, and that in parts of Uganda where elephant and hippo are the major contributors (Field and Laws, 1970). Moreover, the white rhino population in HiP has been restricted by ongoing harvests (Chapter 11), while the elephant population there is still growing (Chapter 14). The densities that might ultimately be attained by these megaherbivores in HiP remain uncertain. Elephants have attained regional densities exceeding two animals/km² in parts of Zimbabwe (Chamaillé-Jammes *et al.*, 2008) and Uganda (Laws *et al.*, 1975) under similar rainfall regimes to HiP, while hippos have reached effective grazing densities exceeding 10 animals per km² in the lakeshore or riparian grasslands that they exploit in Uganda (Field, 1970) and Zambia (Marshall and Sayer, 1976). Other herbivores have continued to coexist at these densities. However, the grazing impacts of white rhinos are more widely distributed away from surface water

than those of hippos, and the grazing lawn grasslands promoted by white rhinos in upland regions would be somewhat less productive than the lawns generated by hippos in riparian margins where both soil moisture and nutrients are concentrated. The only sign of density feedbacks slowing the population increase of white rhinos is a reduction in the overall growth rate from over 9% per year prior to 1970 to around 7% per year currently (Chapter 11). This continuing upward trend highlights the importance of dispersal, enabling the incoming generation of white rhinos to move from regions that are heavily exploited towards places retaining more food. However, dispersal does not ultimately avoid the regulating effects of increased mortality; it only shifts it elsewhere. In the case of HiP, such mortality is pre-empted by live removals within the context of the sink management strategy (Chapter 11).

The high densities attained by white rhinos do not necessarily have a negative effect on effective food availability and hence population growth, because by expanding the extent of grazing lawns white rhinos increase the availability of high-quality forage to the benefit of their reproductive performance. The white rhino population is likely to become limited eventually by the extent of the tall-grass reserves available to support animals through the dry season. However, the fragmentation of tall grasslands by the lawn mosaic restricts the spread of fires and hence the loss of forage for grazers that occurs through incineration (Waldram *et al.*, 2008). The consequences may be beneficial for other grazers, not only for those similarly favouring short grass (wildebeest, warthog) but also for species dependent more on tall grass (buffalo). For the short-grass grazers, white rhinos expand nutritious grazing lawns, but consume much of this grass themselves. For species requiring taller grass, white rhinos pre-empt the loss of this forage to fire while restricting the build up of moribund tissues by fostering annual regrowth.

While conventional wisdom has it that smaller herbivores can out-compete larger ones through being able to survive on sparser forage (Prins and Olf, 1998), white rhinos are not threatened by any smaller grazer because of their capability to crop the shortest grass (Arsenault and Owen-Smith, 2008). Both white rhinos and hippos gain an advantage over smaller species when food is short by being able to survive for longer on their fat reserves, as a consequence of the lower mass-specific metabolic rates (Shrader *et al.*, 2006). Hence, white rhinos neither threaten the coexistence of other grazers, nor are threatened by the latter, at least under the density levels they have attained thus far. This has implications for whether the high biomass densities reached by elephants and hippos

elsewhere would negatively affect the coexistence of other browsers and grazers, especially if wider dispersal is precluded.

In the past, mobile grazers like wildebeest and zebra probably migrated beyond the current boundaries of HiP during the wet season, either towards fertile basaltic soils adjoining the Lebombo hills (see Chapter 2) or towards higher-elevation grasslands where fires lit by humans during the dry season had promoted regrowth. The region near the Mfolozi and Hluhluwe rivers with perennial surface water constituting HiP would have formed a dry season concentration area. This seasonal exodus of mobile herbivores beyond the vicinity of the rivers would have enabled some alleviation of grazing pressure on grasslands during the wet season when grasses are most sensitive to overexploitation. Currently, the year-round grazing by these herbivores coupled with that by sedentary white rhinos plus introduced impala could have negative consequences for the sustainability of grasslands and hence for the herbivore populations dependent on them within the confines of HiP. Thus, the possibility of genuine overgrazing in the form of a reduction in productive capacity of the forage resource cannot be discounted (see Chapter 6).

5.7 Concluding Remarks

Studies on the ecology of white rhinos within HiP, including their interactions with vegetation and other herbivores, have revealed the central role of this mega-grazer in community and ecosystem dynamics. Features shared by white rhinos with other megaherbivores include their dominant contribution to overall herbivore biomass, delayed demographic response to resource depletion and hence dependence on dispersal, capacity to extensively transform structural features of the vegetation, and both competitive and facilitative relationships with other large herbivores (Owen-Smith, 1974, 1988). They function both as keystone species (Owen-Smith, 1987) and as ecosystem engineers (Jones *et al.*, 1997).

Megaherbivores, both grazers and browsers, were formerly present in species assemblages in all continents before the arrival of human hunters with effective weapons (Owen-Smith, 2013b). Observers familiar only with extant ecosystems in northern continents have not fully appreciated the radical changes in both woody and herbaceous vegetation that must have occurred following the extirpation of megaherbivores by human hunting towards the end of the Pleistocene, in association with the effects of climate change. Evidence is progressively revealing the transformation in vegetation structure and fire regimes that have taken place outside

Africa since late Pleistocene times (Owen-Smith, 1987, 1989; Vera *et al.*, 2006; Gill *et al.*, 2009; Johnson, 2009; Rule *et al.*, 2012). The effects of herbivory as well as fire must be adequately taken into account for explaining the global distribution of savannas and other grassy biomes (Bond, 2005). Recognition of the grazing and trampling effects of the extinct herbivore fauna on the herbaceous cover, coupled with nutrient enhancements from their dung, is guiding attempts to restore the grassy steppe that formerly extended from Siberia into Alaska in place of the current shrub tundra (Zimov *et al.*, 1995; Olofsson *et al.*, 2001; van der Wal *et al.*, 2004; Blinnikov *et al.*, 2011). If white rhinos had not been preserved so effectively within HiP, these attempts at ecological restoration would have lacked the observational support documented in this review.

5.8 References

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