Research

Resource partitioning by grass height among grazing ungulates does not follow body size relation

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We compared the grass height grazed by white rhino, wildebeest, zebra and impala through the dry season months in the Hluhluwe–iMfolozi Park in South Africa. We expected that the grass height grazed would increase with the body size of the herbivore species, as suggested from past studies of resource partitioning among large mammalian herbivores. Instead we found that the largest of these species, white rhino, concentrated on the shortest grass, while the smallest species, impala, grazed heights intermediate between those grazed by wildebeest and zebra. Results suggest that the scaling of mouth width relative to body size, and hence to metabolic demands, may be the primary factor governing grass height selection, rather than body size alone. This calls into question the widespread assumption that smaller herbivores are superior competitors through being able to persist on sparser vegetation. Furthermore, there was considerable overlap in grass height grazed among these four species, indicating that niche separation by grass height is inadequate alone to explain their coexistence.

Since the classical study by Bell (1970, 1971) in the Serengeti, it has been widely accepted that resource partitioning among large mammalian grazers occurs partly through differential selection for grass canopy height by herbivores differing in body size (Owen-Smith 1985, Illius and Gordon 1987, Murray and Illius 1996, Arsenault and Owen-Smith 2002). Bell described a grazing succession among species as animals progressively grazed down the grass sward across the catena in the early dry season. Short grasses (and grazing lawns) tend to be predominant on the upper catena where soils are shallowest, and taller grasses become prevalent lower down the slope where soils become deeper and more clayey, and hence retain more soil moisture. The largest species, in this case African buffalo *Syncerus caffer* (body mass 450 kg) moved from the top of the catena as grass height became reduced, followed by zebra *Equus burchelli* (body mass 220 kg), then topi *Damaliscus lunatus* (110 kg) and thereafter wildebeest *Connochetes taurinus* (body mass 165 kg), while Thomson's gazelle *Gazella thomsoni* (body mass 16 kg) remained behind on the short grass left after other species had departed. Bell hypothesized that larger herbivores graze taller grass lower down the catena and facilitate the grazing of smaller herbivores by increasing access to green leaves. This concept drew from an earlier study by Vesey-Fitzgerald (1960), who reported how grazing and trampling by larger grazers facilitated smaller herbivores in tall drainage sump grasslands in southern Tanzania. Bell (1971) noted further how migratory zebra, wildebeest and Thomson's gazelle moved through his study area in order of body size and in relation to declining grass heights.

Grass height has been demonstrated to exert the major influence on bite size, and hence on the food intake rate achieved by grazing herbivores (Laca et al. 1992, Edwards et al. 1995). Hence larger species require longer grass in order to meet their greater quantitative food requirements, while small grazers can still achieve an adequate rate of food intake on very short swards. Following on from this, smaller herbivore species may be superior competitors through being able to survive on grass swards too short or too low in biomass to support larger species (Clutton-Brock and Harvey 1983, Illius and Gordon 1987, Prins and Olff 1998). Short grasses are generally more leafy and hence should be favoured by all herbivores, were it not for the restriction imposed by bite depth on the food intake rate, which is more severe for larger than for smaller animals. On the other hand, larger herbivores are better able to tolerate the poorer quality forage provided by taller grasses (Bell 1971, Geist 1974, Jarman 1974).

Selection for grass height is influenced additionally by the effective mouth width relative to body size, controlling the bite mass and hence rate of food ingestion achieved on grass swards differing in structure (Bell 1969 cited in Owen-Smith 1982, Gordon and Illius 1988, Owen-Smith 1989). A wider mouth increases bite area and compensates to some extent for restrictions on bite depth. For instance, the wide lower incisor arcade of wildebeest enables these animals to maintain a positive energy balance on shorter grass than is the case for more narrow-muzzled topi (Murray and Brown 1993,

Murray and Illius 1996). The two largest grazers, hippo *Hippopotamus amphibius* and white rhino *Ceratotherium simum*, pluck grass with their lips, and have exceptionally wide mouths enabling them to achieve an adequate food intake rate from the nutritious grazing lawns that they promote (Olivier and Laurie 1974, Owen-Smith 1988, Shrader et al. 2006). Nevertheless, their reduced mass-specific metabolic requirements (Illius and Gordon 1992, but see Clauss and Hummel 2005), enables them to exploit taller less nutritious grass when necessary (Owen-Smith 1988).

Despite this emphasis on grass sward height as a factor affecting resource partitioning among large herbivores of different body size, there has been surprisingly little documentation of the grass heights actually selected for feeding by free-ranging animals of these species (Sinclair 1985, Voeten and Prins 1999). Our study was undertaken in the Hluhluwe–iMfolozi Park (HiP) in South Africa, as part of a larger study of resource partitioning within the grazing guild. This area has a large herbivore biomass and diversity approaching that of the Serengeti ecosystem, but with white rhino the dominant species in biomass (Owen-Smith 1988). Our observations were focussed on the dry season when we expected competition to be accentuated as grass height became progressively reduced through grazing. We compared the grass height selected for grazing by white rhino (body mass 1600–2300 kg) with that chosen by zebra, wildebeest and impala *Aepyceros melampus* (body mass 45–70 kg). The first three species are strict grazers, whereas impala are mixed feeders favouring grass for much of the year.

If the grass height selected depended mainly on body size, as suggested by Bell (1970, 1971), the pattern of grass height use depicted in Fig. 1 would be expected. However, the widened bite width of white rhino and wildebeest could enable these two species to exploit shorter grass than might be projected from body size differences alone. Accordingly we expected to find (1) white rhino overlapping broadly with the other three grazers due to their acceptance of both short and tall grass, and (2) wildebeest and white rhino
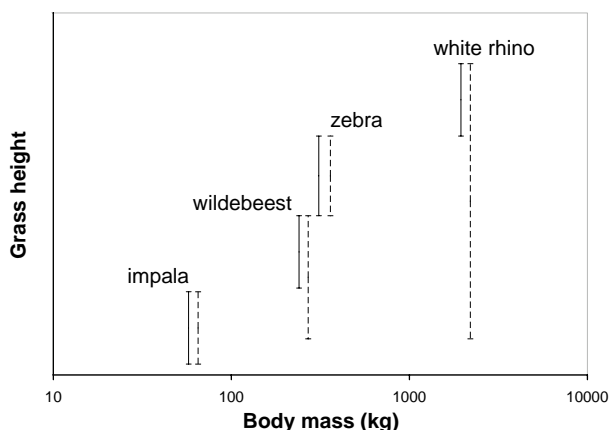

Figure 1. Pattern of grass height use by the herbivore species studied that would be expected considering only body mass differences (—), compared with pattern of grass height use more likely to be expressed considering relative mouth dimensions as well as body size (---).

grazing grass almost as short as that eaten by the somewhat smaller impala (Fig. 1).

Study area

The study was centred on the Mbuzane ranger station in the western iMfolozi section of Hluhluwe–iMfolozi Park, KwaZulu–Natal, South Africa (28°20′S, 31°51′E). The rainfall pattern is characterized by a wet summer from October to March, followed by a dry winter from April to September. Observations on grass height use spanned the dry season months from March to August in 1999, and from May to August in 2000. Rainfall was below average (545 mm) during the first seasonal cycle (October 1998–September 1999), and above average (791 mm) during the second year (October 1999–September 2000), relative to the 690 mm long term mean (1981–1998) for western HiP (KwaZulu–Natal Wildlife authority unpubl.).

White rhino, wildebeest, zebra and impala were among the most abundant grazers in the study area in terms of biomass density. Although buffalo were similarly abundant in biomass, their large herds were encountered too infrequently in the study region for adequate data to be gathered. Waterbuck *Kobus ellipsiprymnus* and warthog *Phacochoerus aethiopicus* were less common grazers.

Methods

Observations were conducted driving a road transect of 49 km, once early in the morning and once in the late afternoon during the main feeding periods of the animals. When an animal or herd was observed feeding within 200 m of the road, the first animal seen grazing was chosen as the focal animal. Its feeding location was identified using nearby landmarks (e.g. trees, bushes, rocks). The herd was then displaced and fresh bites were identified at the site. Fresh bites were readily identified because bitten grass remains white at the 'cut', whereas old bites turn brown very quickly. Animals rarely fed on grass that was completely brown and dry, even during the late dry season. Once a bite was identified, a 1 m² quadrat was placed over the grass patch where feeding by this animal had occurred. Although impala commonly browse shrubs and leaf litter during the dry season, fresh bites on grass were usually found at sites. Observations on impala were discontinued in 2000 in order to concentrate data collection on the remaining three species.

Feeding observations amounted to 20–30 records per species per month, leading to the following total sample sizes: white rhino – 215; zebra – 245; wildebeest – 246; impala – 117. For analysis, the early (March–May) and late (June–August) periods of the 1999 dry season were distinguished. In 2000, grasses remained as green through August as they had been around May 1999, hence no seasonal subdivision was made.

Each grass species present within the 1 m² quadrat was identified and recorded, as well as the grass species that was eaten. Based on the predominant species in the sward, feeding patches were assigned to four grassland types, following Downing (1972) and Owen-Smith (1973).

Grazing lawns were characterised by short or stoloniferous grass species, including *Urochloa mosambicensis, Panicum coloratum, Digitaria argyograpta, Sporobolus nitens* and *Cynodon dactylon. Themeda* grasslands consisted mainly of the medium–tall bunch grasses *Themeda triandra, Cymbopogon plurinodis* and *Heteropogon contortus*. Woodland or shade grasslands comprised mainly relatively tall *Panicum maximum, P. deustum* and *Enteropogon monostachyus*. An 'other' grassland category included mostly *Bothriochloa insculpta, Eragrostis* spp., *Cenchrus ciliaris* and *Setaria* spp. Since only the grass heights presented by grazing lawns were distinct from those of other grassland types, the latter were combined into a medium–tall grassland category, encompassing *Themeda*, woodland and other grassland types, for analysis.

The proportion of green grass compared to brown grass (all grass parts, stem, culm, leaves) in the quadrat was categorized as a percentage using Walker's (1976) eight-point scale: 0, 1–10, 11–25, 26–50, 51–75, 76–90, 91–99 or 100% green.

Within each sample quadrat, the height of the grass plant eaten left after the bite was recorded using a ruler. In addition, the leaf canopy height of nearly ungrazed plants of the same grass species was recorded and assigned to four height categories for analysis: <5 cm, 6–10 cm, 11–20 cm and ≥ 21 cm.

Data analysis

Log linear analysis was undertaken using Statistica 2000 to examine distinctions among the herbivore species in their relative use of (1) grass height (four categories), (2) grassland type (two categories) and (3) grass height within each of the two grassland type categories. Period (three seasonal distinctions) was considered as an additional factor. To test which factors and interactions contributed to the patterns observed, saturated three-way models (e.g. herbivore × height × period), were compared with models omitting each factor and interaction, considering the omission significant if $p < 0.05$.

As a descriptive measure of the extent of overlap in height use between species pairs, Pianka's (1973) index was calculated: $O_{jk} = O_{kj} = \Sigma P_{ij} \times P_{ik}/\sqrt{\Sigma P_{ij}^2 \times \Sigma P_{ik}^2}$, where O_{jk} and $O_{kj} =$ degree of overlap between species j and k, and P_{ij} and $P_{ik} =$ proportions of resource i used by species j and k species respectively.

The muzzle width index was calculated by dividing the incisor breadth of impala (3.2 cm), wildebeest (6.95 cm) and zebra (5.26 cm) by the cube root of body mass in kg (Murray and Illius 1996). Because white rhinos lack lower incisors and crop with their lips, their measured bite width (20 cm, Owen-Smith 1988) was used instead for the calculation.

Results

Grass height use

While grass height grazed differed significantly among the four herbivore species ($\chi^2 = 113.19$, DF $= 27$, p $= 0.001$), the height of grass grazed did not differ among the three periods ($\chi^2 = 29.46$, DF $= 24$, p $= 0.203$). Hence grass height use could be compared among the herbivores without needing to take into account the dry season period when observations were made. Greatest proportional use of grass shorter than 5 cm was shown by white rhino ($>50\%$ of records), and least use of this height class by zebra (Fig. 2). Correspondingly, zebra made relatively the most use of grass taller than 20 cm, and white rhino the least.

In pair-wise comparisons, white rhino grazed significantly different grass heights than zebra ($\chi^2 = 87.33$, DF $= 3$, p < 0.001), wildebeest ($\chi^2 = 20.10$, DF $= 3$, p < 0.001) and impala ($\chi^2 = 32.71$, DF $= 3$, p < 0.001). The grass heights grazed by wildebeest and zebra also differed significantly ($\chi^2 = 29.36$, DF $= 3$, p < 0.001). Although zebra appeared to graze less short grass and more tall grass than impala, this difference was not significant ($\chi^2 = 4.75$, DF $= 3$, p $= 0.191$). Both species showed a modal grass height grazed of 11–20 cm, whereas for wildebeest the modal grass height class was <5 cm (Fig. 2).

Calculations of overlap indices confirmed that zebra and impala were most similar in grass height grazed (0.90), while wildebeest overlapped strongly with impala (0.87), zebra (0.85) and white rhino (0.89). Overlap was least between the two non-ruminants, white rhino and zebra (0.68).

Use of grassland types

The grassland type grazed differed among periods ($\chi^2 = 108.59$, DF $= 24$, p < 0.001), as well as among the herbivore species ($\chi^2 = 76.29$, DF $= 27$, p < 0.001) (Fig. 3). All herbivore species except impala tended to graze less short grass species (i.e. grazing lawns) during the later part of the 1999, compared to the earlier dry season months of this year, although when considered individually the difference was significant only for wildebeest ($\chi^2 = 11.63$, DF $= 1$, p < 0.001). In addition, white rhino, zebra and wildebeest appeared to use grazing lawns more during the dry season of 2000 than in the corresponding periods of the drier year of 1999.

Considering pair-wise comparisons, zebra used grazing lawns significantly less than wildebeest in the early dry
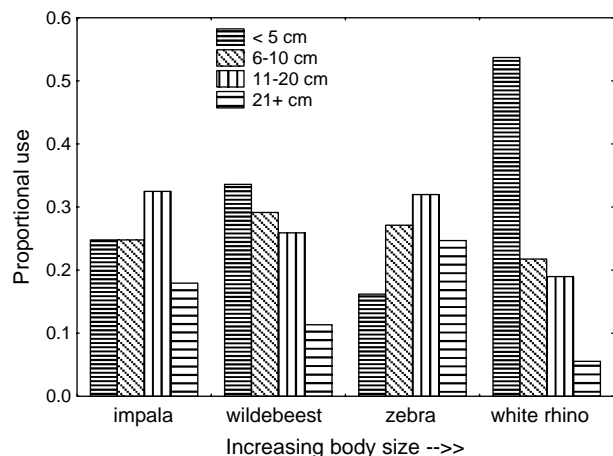

Figure 2. Relative use of grass height categories by impala, wildebeest, zebra and white rhino.
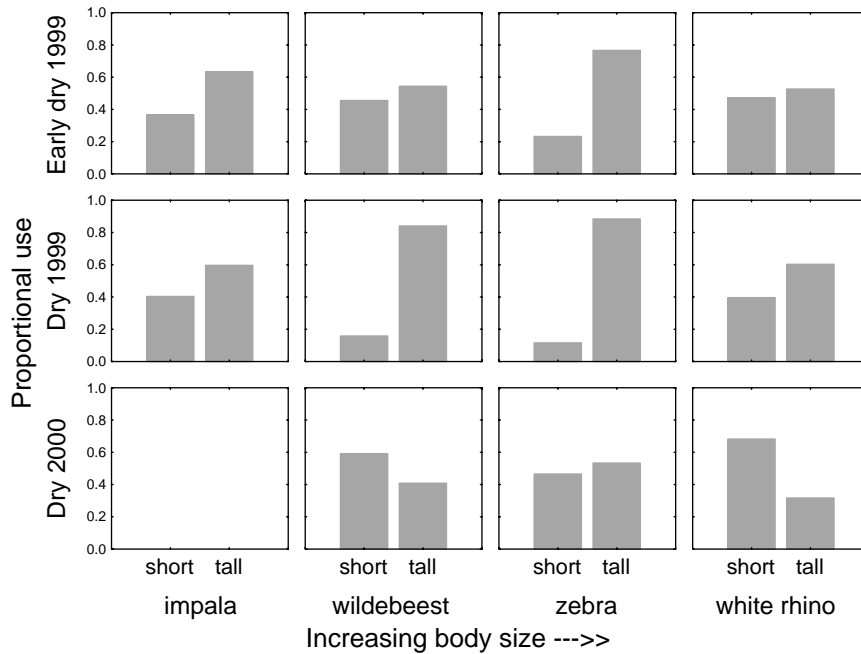
Figure 3. Seasonal use of grazing lawns ('short') and medium–tall grasslands ('tall') by impala, wildebeest, zebra and white rhino.

season of 1999 ($\chi^2 = 7.75$, DF $= 1$, p < 0.005), but during the later part of this dry season wildebeest made considerably more use of medium–tall grassland and appeared similar to zebra (Fig. 3). The apparently greater use of grazing lawns by white rhino compared with zebra was significant during early dry season of 1999 ($\chi^2 = 7.98$, DF $= 1$, p < 0.005). White rhino and impala, and during the early dry season also wildebeest, appeared similar in their fairly even use of both lawns and taller grassland in 1999. Zebra made relatively greater use of grazing lawns in 2000 than in 1999 ($\chi^2 = 23.81$, DF $= 1$, p < 0.001), but

still grazed medium–tall grasslands more frequently than white rhino ($\chi^2 = 10.458$, DF $= 1$, p < 0.001).

Grass height use within grassland types

Grass height grazed differed significantly among the herbivore species both when feeding in grazing lawns ($\chi^2 = 38.06$, DF $= 9$, p < 0.001) and in medium–tall grasslands ($\chi^2 = 35.60$, DF $= 9$, p < 0.001) (Fig. 4). In grazing lawns, white rhino, and to a lesser extent wildebeest and
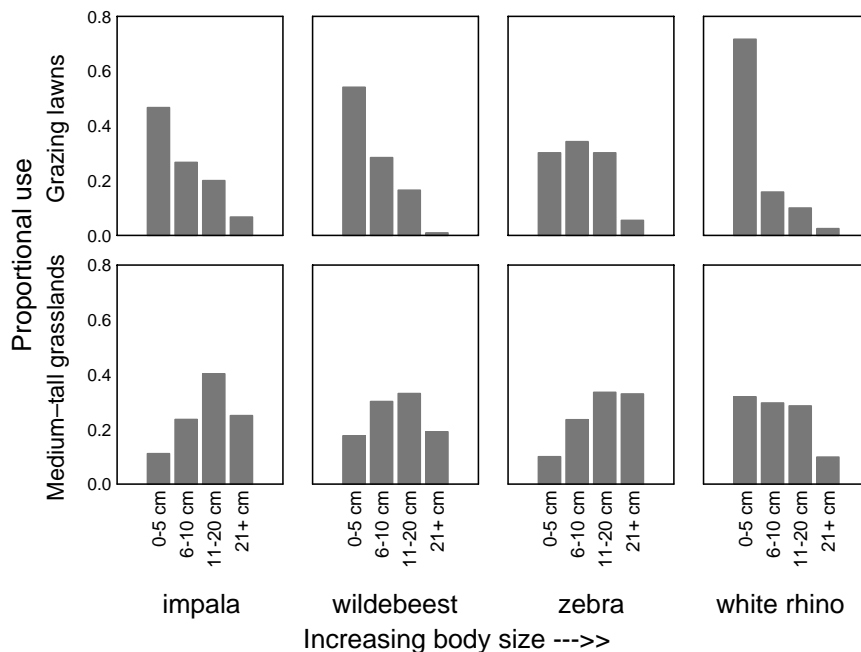

Figure 4. Relative use of grass height within grassland categories by impala, wildebeest, zebra and white rhino.
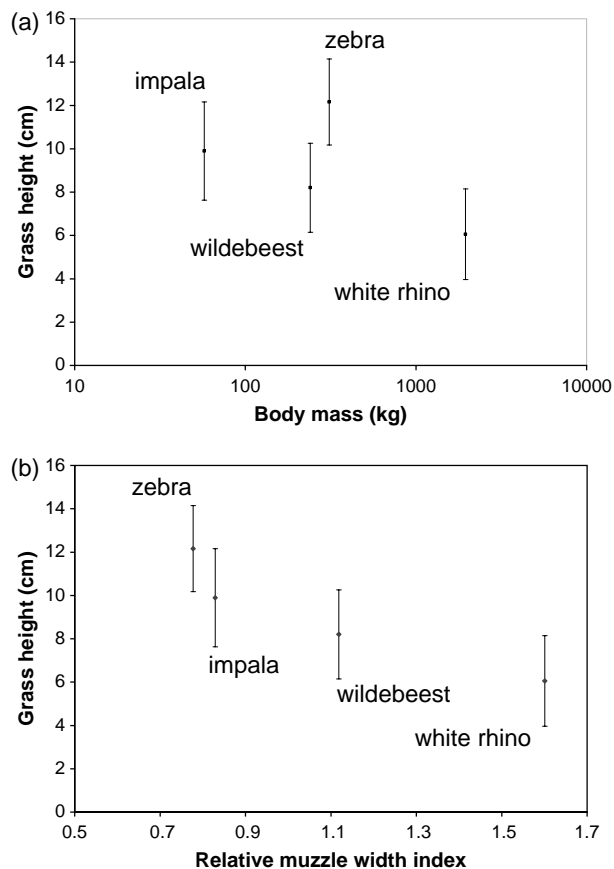
Figure 5. (a) mean and SD of grass height use (cm) by the herbivores in relation to body mass (kg). (b) mean and SD of grass height use (cm) by the herbivores in relation to the relative muzzle width index (effective bite width (cm)) (from Murray and Illius 1996, Owen-Smith 1988))/cube root of body mass (kg).

impala, concentrated on grass <5 cm, while zebra showed an even use of height categories up to 20 cm. In medium–tall grassland, white rhino tended to neglect grass taller than 20 cm, while wildebeest and impala grazed a modal grass height of 11–20 cm, and zebra grazed grass height categories taller than 10 cm evenly.

Discussion

Our findings show that the grass height grazed by impala, wildebeest, zebra and white rhino, did not simply follow the pattern expected from body size differences (Fig. 5a). The largest species, white rhino, consistently utilized shorter grass than the three smaller grazers. Moreover, the smallest species, impala, tended to use grass heights intermediate between those grazed by wildebeest and zebra. Nevertheless, wildebeest generally used shorter grass than zebra. Hence the observed pattern of grass height use corresponded instead with relative bite width as depicted in Fig. 5b. While seasonal conditions seemed not to influence the grass height grazed by these herbivores, their relative use of grazing lawns versus taller grass types did depend on the prevailing conditions. Zebra made relatively greatest use of grazing lawns during the higher rainfall year when the grass

on offer in these lawns was tallest. Wildebeest largely abandoned grazing lawns towards the end of the dry season of the drier year. However, even when feeding in the same grassland type these herbivores differed in the grass heights that they selected for grazing.

In the Serengeti–Mara region of east Africa, wildebeest were generally found in grass stands about 10 cm tall at the end of the wet season, while zebra utilized stands of height 25 cm, as did impala (Sinclair 1985). By the mid-dry season two months later, wildebeest had spread their use evenly across stands 10–25 cm tall, whereas zebra had shifted towards grass swards 50 cm in height or taller. Impala concentrated on short grass swards about 10 cm in height, while Thomson's gazelle consistently utilized even shorter grass swards. These estimates were made from a vehicle, and represent the predominant height of the available grass at sites where animals were observed, not the grazed height as shown in our study. In the Tarangire region of Tanzania, grass height post-grazing during the wet season was 3–8 cm for wildebeest compared with 9–14 cm for zebra (Voeten and Prins 1999). In the dry season, these wildebeest grazed grass to 11–16 cm versus 17–30 cm for zebra. In northern Botswana, zebra moved off in search of taller grass after sward height had been reduced to 20 cm (Joos-Vanderwalle 2000 reported in Owen-Smith 2002). Our observations on the difference in grass height favoured by wildebeest and zebra are consistent with these findings from other studies.

The mean grass height grazed by white rhino during a study conducted in HiP between 1968 and 1971, increased from 10 cm in the early dry season to 24 cm by the late dry season (Owen-Smith 1988). Associated with this was a shift from around 50% use of grazing lawns at the start of the dry season to 70–90% use of medium–tall Themeda grassland by August. The conditions at the time of these observations were generally drier than during our study years and the white rhino population and hence grazing pressure larger. Under our study conditions, white rhinos used grass shorter than 10 cm throughout the dry season (Shrader et al. 2006).

From observations on tethered animals, Murray and Brown (1993) found that young wildebeest (body mass 86–108 kg) maximized their food intake rate on grass heights of around 5 cm. Thomson's gazelles (body mass 25 kg) seemed to obtain highest nutritional gains from a grass biomass of 25 g m^{-2}, associated with a grass height of around 5 cm (Wilmshurst et al. 1999), similar to that reported for wildebeest. On taller swards, the food intake rate of the gazelles did not increase further, while the digestibility of the material consumed deteriorated. Extending these findings, Wilmshurst et al. (2000) projected an increase in the optimal sward biomass (and hence height) with increasing herbivore size. Similarly, Prins and Olff (1998) depicted smaller grazers as achieving their specific energy requirements from a lower grass biomass than larger species.

Our observations on impala and white rhino were inconsistent with the projected trend towards an increase in the grass biomass and hence height favoured with increasing herbivore body size. For white rhino (as for hippo), it has been widely recognised that their exceptionally broad muzzles and lip-plucking technique enable them to feed efficiently on very short grass swards, despite their large size (Olivier and Laurie 1974, Owen-Smith 1988,

Murray and Illius 1996). Impala as mixed feeders consuming both grass and browse have a relatively narrow incisor breadth (Murray and Illius 1996, Perez-Barberia and Gordon 2001). This enables them to selectively pluck individual leaves from relatively tall grass tufts (observations made at close quarters on hand-reared animals by Owen-Smith), and thus feed effectively across a range of grass heights.

Duncan (1975) and Murray and Illius (2000) noted how topi with a narrower muzzle than wildebeest can selectively remove the green leaf component from medium-height grass swards. Among the smallest grazers, mountain reedbuck *Redunca fulvorufula* (body mass 25–30 kg) and oribi *Oerebia oerebi* (body mass 13–20 kg) occur largely in tall grassland habitats and feed mainly on fairly tall grass tufts (Irby 1977, Oliver et al. 1978, Reilly et al. 1990), ingesting mostly leaf tissues (Owen-Smith and Cumming 1993). Owen-Smith (1985) modelled the combined consequences of differences in both body mass and relative bite dimensions, illustrating how a medium-sized but relatively wide-mouthed ruminant like wildebeest can perform best when feeding in short grass swards, while smaller ruminants with absolutely smaller bite dimensions could feed most effectively in relatively tall grass, through selectively plucking green leaves.

Accordingly, we propose that the scaling of the bite dimensions, indexed by dividing the effective bite width (i.e. the breadth of the incisor arcade for ruminants) by the cube root of the body mass, has the overriding influence on the grass height favoured for grazing, rather than body size (Fig. 5a–b; Owen-Smith 1988, p. 90). The most important influence of body mass is on the metabolic scaling of nutritional requirements, which enables larger herbivores to tolerate taller grass swards with generally lower nutrient contents because of greater prevalence of structural fibre (Bell 1971, Geist 1974, Jarman 1974). Nevertheless, very large herbivores may still utilize very short grass swards through adaptations enabling them to feed effectively under such conditions, while much smaller herbivores may graze quite tall grass swards by selectively plucking the green leaf component from among surrounding stems. This interpretation also calls into question the assumption that the smallest herbivores should be the superior competitors through being able to persist on the sparsest vegetation (Clutton-Brock and Harvey 1983, Illius and Gordon 1987, Gordon and Illius 1988, Prins and Olff 1998). This may be true under some conditions, but in different circumstances the largest herbivores can survive when only poor quality albeit abundant vegetation remains. Hence, in explaining resource partitioning among syntopic large grazers, the allometric scaling of both intake rate, controlled largely by bite dimensions in relation to grass height, and nutritional requirements, governed fundamentally by the mass-specific metabolic rate, must be taken into account.

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