Resource partitioning among African savanna herbivores in North Cameroon: the importance of diet composition, food quality and body mass

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Abstract: The relationship between herbivore diet quality, and diet composition (the range of food plants consumed) and body mass on resource partitioning of herbivores remains the subject of an ongoing scientific debate. In this study we investigated the importance of diet composition and diet quality on resource partitioning among eight species of savanna herbivore in north Cameroon, with different body mass. Dung samples of four to seven wild herbivore and one domesticated species were collected in the field during the dry and wet period. Diet composition was based on microhistological examination of herbivore droppings, epidermis fragments were identified to genus or family level. In addition, the quality of the faecal droppings was determined in terms of phosphorus, nitrogen and fibre concentrations. The results showed that there was no significant correlation between body mass and (differences in) diet composition for wet and dry season. When all species are considered, only significant relationships are found by the Spearman rank correlation analyses during the wet season between body mass and phosphorus and nitrogen, but this relationship did not exist during the dry season. When the analyses focuses on ruminants only (thus leaving out hippo), none of the relationships between body mass and diet quality was significant in either season. During the dry season the proportion of graminoids ranged between 10% (small unidentified herbivore species) to 90% (hippopotamus), during the wet season this proportion ranged from 60% (zebu) to 90% (hippopotamus). All species but zebu had more graminoids in their dung during wet season compared with dry season. However all species but hartebeest had more graminoids old stems in their dung during the dry season, compared with the wet season. The niche breadth for food categories consumed by kob (0.300), hippo (0.090), hartebeest (0.350), roan (0.510) and zebu (0.300) was much greater in the dry season than in the wet season for kob (0.120), hippo (0.020), hartebeest (0.190), roan (0.090) and zebu (0.200). When looking at grass taxa consumed, the niche breadth of kob (0.220), hartebeest (0.140), and roan (0.250) was also greater in the dry season when compared with the wet season for kob (0.050), hartebeest (0.120) and roan (0.120). The opposite was found for zebu and hippo. Comparison of the species' diet compositions with randomized data showed that dietary overlap between different herbivore species was much higher than what would be expected on the basis of chance, demonstrating surprisingly limited niche separation between species. This offers potential for competition, but it is more likely that the high niche overlap indicates absence of competition, due to low herbivore densities and abundant food resources, permitting species to share non-limiting resources. With increasing herbivore densities and subsequent increasing scarcity of resources, the relationship between diet quality and body mass in combination with increased niche separation is expected to become more visible.

Key Words: competition, dietary overlap, faecal analysis, herbivores, savanna ecosystems, ungulates

INTRODUCTION

Resource partitioning among potential competitors takes a central place in ecological research. Grass-eating herbivores have received much attention in these studies

because of the high numbers of coexisting species, in particular in Africa (Cromsigt & Olff 2006, Prins & Olff 1998, Prins *et al.* 2006). Around 100 species of herbivore larger than 2 kg occur in Africa that feed to a greater or lesser extent on grass (Prins & Olff 1998), and various studies have argued that African grazer assemblages are structured by patterns of resource partitioning among potential competitors (Arsenault & Owen-Smith 2002).

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MacArthur & Levins (1967) proposed a simple model to explain species richness as a function of resource availability and niche relationships among species. Based on this niche theory, one might expect the habitat–niche width to decline with an increasing number of sympatric species and decreasing resources. Demment & Van Soest (1985) showed that body size of herbivores shows a relationship along a resource axis of grasses having different quality, expressed as fibre contents. Gut capacity increases linearly with body mass (Clauss *et al.* 2007, Demment 1982, Demment & Van Soest 1985), whereas energy requirements (expressed as metabolic body size) scale with actual body weight as $W^{0.75}$ (Kleiber 1975). Since the ratio of metabolic requirements to food processing capacity decreases with increasing size, various authors have argued that smaller-sized herbivores need food of a higher quality than do larger herbivores (Demment & Van Soest 1985, Jarman 1974, Prins & Olff 1998). However, the body mass–food quality relationship has recently been challenged. Pérez-Barberia *et al.* (2004) could find no significant effect of body mass of ruminants on fibre digestibility, in contrast to previous studies (Iason & Van Wieren 1999, Robbins *et al.* 1995). In addition, Clauss *et al.* (2007) argued that gut retention time is largely independent of body mass in grazing ruminants, so that a larger body mass does not necessarily lead to improved digestive efficiency.

In a recent study of the ungulate assemblage of Kruger National Park, South Africa, Codron *et al.* (2007) showed a significant negative correlation between body mass and the percentage nitrogen (N) in the faeces of herbivores. In addition, evidence was found of a positive relationship between the body mass of antelopes and buffalo (family Bovidae) and fibre concentrations of the faeces (Codron *et al.* 2007). Although these findings are in line with the idea that body mass differences facilitate niche differentiation among sympatric herbivores (the Jarman–Bell principle; Bell 1971, Jarman 1974), no relationship was found between herbivore body mass and diet type (grass versus browse proportions in diet) (Codron *et al.* 2007).

Numerous studies have investigated patterns of resource partitioning among grazing herbivores (Cromsigt & Olff 2006, Mysterud 2000, Prins *et al.* 2006, Putman 1996, Voeten & Prins 1999, Wegge *et al.* 2006). However, the majority of studies tried to interpret patterns of niche separation based solely on diet composition. Diet can be interpreted as the range of food plants consumed by herbivores. However, the range of food plants found in the diet is not informative about the quality of the food that is consumed. In this study we will test the hypothesis that diet quality will decrease with increasing body mass. We will take an integrative approach to diet composition, niche overlap and food quality to investigate patterns of resource partitioning, and we relate these patterns to the body masses of herbivore species. This is done for an ungulate assemblage in the little-studied Guinea savanna zone of West Africa that is characterized by comparatively nutrient-poor soils and high rainfall.

MATERIALS AND METHODS

Study area

This study was carried out in Bénoué National Park (1800 km²; 7°55′–8°40′N, 13°33′–14°02′E) in north Cameroon. The area has an annual rainfall of 1200−1500 mm, unimodally distributed from April to October. Poor ferruginous soils prevail (Brabant & Humbel 1974). The park lies within the northern Guinean savanna zone and is characterized by five major plant communities: *Isoberlinia doka* woodland savanna, *Anogeissus leicocarpus* riparian forest, *Terminalia laxiflora* and *T. macroptera* open savanna, and *Burkea-Detarium* open savanna (Stark & Hudson 1985). Dominant grasses include species of *Andropogon*, *Hyparrhenia* and *Loudetia*. Bénoué NP is home to 17 species of ungulate (Klop & Van Goethem 2008; Table 1), which are mostly associated with open wooded savanna and riparian vegetation. By far the most common ungulate species in the Bénoué region is Western kob *(Kobus kob)*, whereas other common species include oribi (*Ourebia ourebi*), red-flanked duiker (*Cephalophus rufilatus*) and Western hartebeest (*Alcelaphus buselaphus major*) (Klop *et al.* 2007, Mayaka 2002). This study was conducted in two phenological periods: halfway through the dry season, between 7 February and 18 March (hereafter referred to as dry period), when the grass layer consisted mainly of post-fire regrowth, and early in the rainy season, between 1 and 8 June (hereafter called the wet period) when the grass had reached a height of 15–20 cm.

Dung collection and sampling

Diet composition and diet quality of the different herbivores were assessed from dung samples (De Jong *et al.* 1995, 2004). Dung samples of seven wild herbivore species (Western kob *Kobus kob*, Western hartebeest *Alcelaphus buselaphus major*, Defassa waterbuck *Kobus ellipsiprymnus defassa*, roan *Hippotragus equinus*, buffalo *Syncerus caffer*, hippopotamus *Hippopotamus amphibius* and one unidentified species) and one domesticated species (Zebu cattle *Bos indicus* Linn.) were collected in the field during the dry period. A total of 4–11 dung samples per species were collected during the dry season and during the early wet season. Based on the size and shape of the droppings the unidentified species must refer to either oribi, common duiker or red-flanked duiker. In the wet season, dung sample collection was restricted to

Table 1. The 17 species of ungulate recorded in Bénoué National Park. Zebu (*Bos indicus* Linnaeus, 1758; 250 kg) is a domesticated species and not included in the Table. Body mass data are taken from Kingdon (1997) and refer to the average weight of male and female, rounded to the nearest kg.

Common name	Species	Body mass (kg)	Guild
Red-flanked duiker	*Cephalophus rufilatus* Gray	10	Browser
Oribi	*Ourebia ourebi* Laurillard	17	Grazer
Common duiker	*Sylvicapra grimmia* Linnaeus	17	Browser
Bohor reedbuck	*Redunca redunca* Pallas	47	Grazer
Bushbuck	*Tragelaphus scriptus* Pallas	49	Browser
Red river hog	*Potamochoerus porcus* Linnaeus	80	Omnivorous
Warthog	*Phacochoerus africanus* Gmelin	83	Grazer
Kob	*Kobus kob* Erxleben	86	Grazer
Korrigum	*Damaliscus lunatus korrigum* Burchell	127	Grazer
Hartebeest	*Alcelaphus buselaphus major* Pallas	161	Grazer
Waterbuck	*Kobus ellipsiprymnus defassa* Ogilby	215	Grazer
Roan	*Hippotragus equinus* Desmarest	261	Grazer
Derby's eland	*Taurotragus derbianus* Gray	539	Browser
Buffalo	*Syncerus caffer* Sparrman	550	Grazer
Giraffe	*Giraffa camelopardalis* Linnaeus	1340	Browser
Hippopotamus	*Hippopotamus amphibius* Linnaeus	1715	Grazer
African savanna elephant	*Loxodonta africana* Blumenbach	4000	Mixed Feeder

five species (kob, hartebeest, zebu, roan, hippopotamus). The more limited number of species from which dung samples were obtained in the wet season was due to the difficulties in finding dung in the high grass during the wet season. Dung samples were identified by the researchers themselves and often collected after having seen the animal defecating. Older dung samples were compared with fresh samples that were identified with certainty, based on the size, shape and indentation of the pellets. Samples were then double-checked (blind test) by experienced local trackers and finally checked again, using Stuart & Stuart (2000). In the dry period dung in the field dried out quickly, so that the structure of the plant material remained intact. Samples were taken from dung that was estimated to be less than 2 wk old. According to Leslie *et al.* (2007) exposure of faeces to weather or insects does not compromise retention of N for 2–3 wk post defecation. In the wet period dung decay rate was high, so that only fresh dung (up to 3 d old) was collected. All samples were air dried. For each period, the samples were pooled per herbivore species, further dried and sterilized by repeated heating at 100 °C. Two parallel sets of subsamples were then taken, one set for microhistological and another for chemical analysis. According to Van Soest (1994) air-dried dung can be heated to 100 °C without any significant disturbance of N content measurements by Maillard reactions.

Diet composition

Diet composition was based on microhistological examination of herbivore droppings (De Jong *et al.* 1995, 2004). Microhistological examination provides an estimate of the ingested biomass per plant taxon, based on the assumption that the surface/dry matter ratio of leaves is more or less constant in different species (Cid & Brizuela 1990, Sparks & Malechek 1968, Stewart 1967). Samples for microhistological analysis were softened and further sterilized by autoclaving with some water for about 8 h at 125 °C, then thoroughly mixed and washed in a Waring Blender, strained over a 0.1-mm plankton sieve and stored in 70% ethanol. From every mixed sample ten random grab samples were examined by light microscopy and measured by using a grid of 0.01-mm^2 squares in the microscope eyepiece. At least 100 fragments of cuticle or epidermis were identified by comparison with photomicrographs of epidermal material in a reference collection, as detailed elsewhere (De Jong *et al.* 1995, 2004). Over 60 species of food plant, mostly grass species occurring in the region, were sampled for reference slides. Epidermis fragments smaller than 0.01 mm^2 were ignored as they do not always carry enough features to make identification conclusive. Epidermis fragments were identified to genus or family level. The abundance of each taxon was calculated as a percentage of the total area of the fragments measured (Alipayo *et al.* 1992, Cid & Brizuela 1990, Homolka & Heroldová 1992, Putman 1984, Sparks & Malechek 1968, Stewart 1967).

Diet quality

The quality of the faecal droppings in terms of N and P and fibre contentrations may give indications of the differences in the quality of the plants consumed by the different herbivores. Neutral Detergent Fibre (NDF%) concentration was determined, using 0.5 g of faecal material. NDF is a measure of fibre concentration of the faeces, so high NDF values mean low digestibility of the

diet. NDF was determined using the ANKOM filter bag procedure (ANKOM Technology Macedon. NY, USA) with omission of the sodium sulphite and the heat resistant α-amylase. Neutral Detergent Solution was prepared following Goering & Van Soest (1970).

The faecal samples were dried at $100\,^{\circ}$C, weighed and burned to determine the inorganic concentration. The N and P concentration of samples was determined by using a modified Kjeldahl destruction. Since all dung samples were pooled per species per period, no measure of variance could be calculated.

Resource overlap

We studied the resource overlap between the different herbivores at two levels, namely: (1) individual taxa (species, genus, or higher level) consumed, and (2) food categories. The latter consisted of six groups: graminoids, graminoid old stems, Caesalpiniaceae leaves, other dicot leaves, Caesalpiniaceae flower buds, and miscellaneous. Resource overlap among the herbivores was quantified using the index of Pianka (1973), where complete resource overlap (identical diets) results in a score of 1.0 and a completely different diet would result in a score of 0.0 (Legendre & Legendre 1998, Pianka 1973). To assess whether differences in resource use between two species were significant, we compared the calculated Pianka's index to a reference value for resource overlap based on a randomization procedure of our data. This reference value is the amount of resource overlap that is expected on the basis of chance alone, and was calculated as the mean resource overlap from 5000 randomized matrices of diet composition using the program EcoSim. At the plant taxon level the reference value (mean $\pm$ SD) was 0.17 ± 0.09 in the dry season or 0.16 ± 0.05 in the wet season; when the food items were grouped into categories the reference value was 0.40 ± 0.05 in the dry season or 0.27 ± 0.04 in the wet season. Thus, we considered values of Pianka's index lower than the reference values indicative of significantly different diets.

The niche breadth of plant taxa and food categories consumed by a particular herbivore species was assessed using Levins' measure (Levins 1968):

$$B = 1 / \sum p i^2$$

where B is the niche breadth and p_i is the proportion of plant taxon or food category i in the diet (Levins 1968). This index was standardized to a scale of $0-1$ following Hurlbert (1978):

$$Bs = (B - 1)/(n - 1)$$

where n is the total number of taxa or food categories consumed by at least one herbivore species. The relation

between body mass and diet composition was investigated using a Mantel test (Legendre & Legendre 1998). This test was used to quantify the correlation between a dietary dissimilarity matrix and a body mass dissimilarity matrix. Correlation between herbivore body mass and diet quality, i.e. fibre concentration (expressed as neutral detergent fibre (NDF), i.e. total cell wall concentration), percentage nitrogen and percentage phosphorus in the faeces, was investigated using Pearson correlation coefficients. The observed dietary overlap was also compared to the extent of overlap that could be expected on the basis of chance alone, using a randomization procedure of resource use matrices as described above. The mean observed resource overlap in Bénoué NP was then compared to the mean resource overlap from 5000 randomized matrices.

Deviation from randomness was considered significant when the observed diet overlap fell in the extreme upper or lower tail (each set at 2.5%) of the range of simulated overlap values.

RESULTS

Diet composition

Graminoids formed the major share of the dung samples of all herbivores except the small unidentified herbivore species (Figure 1). During the dry season the proportion of graminoids ranged between 10% (small unidentified species) to 90% (hippopotamus), during the wet season this proportion ranged from 60% (zebu) to 90% (hippotamus). All species but zebu had more graminoids in their dung during the wet season compared with the dry season. However, all species but hartebeest had more graminoids old stems in their dung during the dry season, compared with the wet season. Also in the early wet season very soft grass cuticles were found in all dung samples, especially of *Andropogon* species, which were less present in the samples from the dry season. Leaf sheath or stem fragments have far less specific patterns than leaves; they were noted as 'grass', together with leaf fragments that could not be identified. Thick-walled fragments of dry stems and leaf sheaths which occurred in all faecal samples along with grass fragments of better quality were noted separately as 'graminoid old stems' (Figure 1).

Besides grasses, most dung samples contained pulpy tissue with epidermis resembling flower buds or fruit pods of *Isoberlinia doka*, the dominant tree in the region. In addition, in the dry season most samples also contained *I. doka* leaves. *Isoberlinia doka* leaves were found most in faeces of migrating domestic cattle, probably from branches that local herdsmen chop off. In the early wet season, *I. doka* leaves were absent from all dung samples but pods were present, especially in cattle dung. Again, these could have been knocked down by herdsmen. We
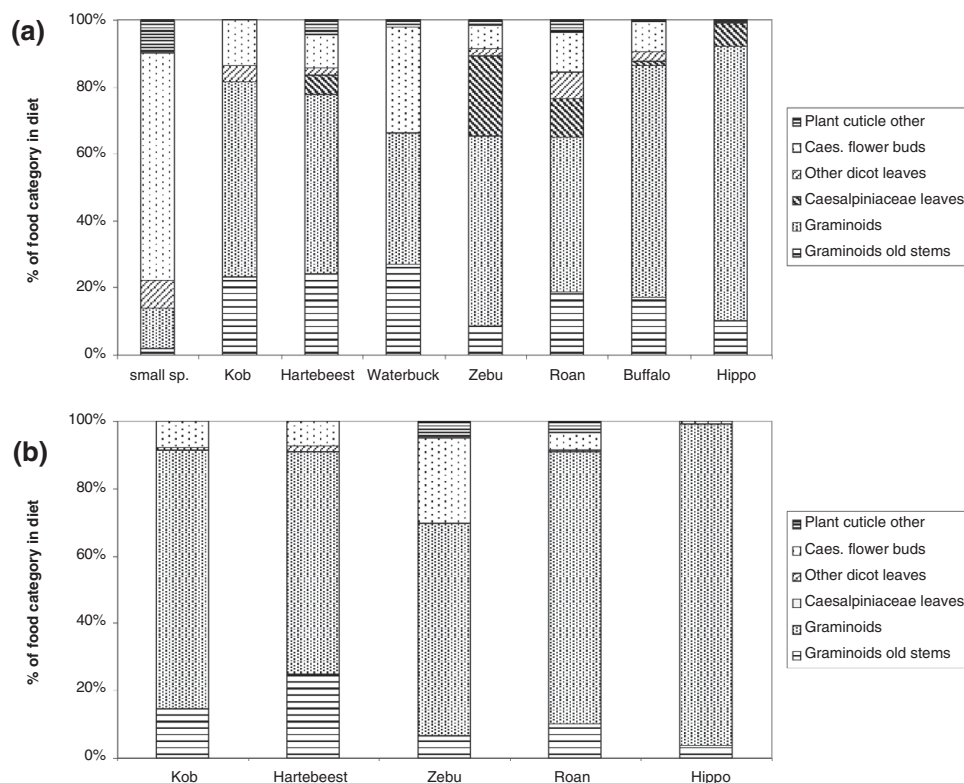
Figure 1. Diet composition of herbivores in Bénoué N. P. during the dry (a) and wet (b) season. Plant cuticle other = all other plant cuticles, which were not identified; Caes flower buds = Caesalpiniaceae flower buds; Other dicot leaves = fragments of all other dicotyledon leaves which were not identified; Graminoids = fragments identified as green graminoids; Graminoids old stem = fragments identified as old yellow graminoids.

could not identify any of the seed parts found in the dung. In the dry season, no fruits were present but fleshy flower buds with similar structures were (Figure 1), as trees start flowering in March. *Isoberlinia doka* buds were the main part of the diet of the unidentified small herbivore species. Based on the high proportion of browse in the diet, this species must have been either common or red-flanked duiker. Oribi, the only other small herbivore in the area, can be ruled out because this species is predominantly a grazer.

Resource partitioning

In the dry season, the diet of the unidentified small herbivore species was different from all other species except waterbuck at both the taxon level and the food category level (Table 1), because of its low grass percentage and high percentage of *I. doka* buds. Waterbuck also differed from zebu and hippo at the taxon level, but showed no differences at the category level. There were no significant differences between the diets of

all other species, at the taxon and the category level in both the dry and wet season (Tables 2 and 3).

The niche breadth for food categories consumed by kob (0.300), hippo (0.090), hartebeest (0.350), roan (0.510) and zebu (0.300) was much greater in the dry season than in the wet season for kob (0.120), hippo (0.020), hartebeest (0.190), roan (0.090) and zebu (0.200) (Figure 2a). When looking at grass taxa consumed, the niche breadth of kob (0.220), hartebeest (0.140) and roan (0.250) was also greater in the dry season when compared with the wet season for kob (0.050), hartebeest (0.120) and roan (0.120). The opposite was found for zebu and hippo, with a smaller niche breath for zebu (0.100) and hippo (0.060) in the dry season compared with the wet season for zebu (0.200) and hippo (0.210) (Figure 2b).

A Mantel test showed that there was no significant correlation between body mass and (differences in) diet composition, either for the dry season (taxon level: $Z = 0.19$, $P = 0.72$; category level: $Z = 0.15$, $P = 0.66$) or the wet season (taxon level: $Z = 0.41$, $P = 0.81$; category level: $Z = 0.43$, $P = 0.82$). Omitting the unidentified small herbivore species (i.e. common or

Table 2. Resource overlap (expressed as Pianka's index) between species pairs of herbivores at both the food category level (upper right half of matrix) and the grass taxon level (lower left half) in the dry season. The number of samples refers to the number of pellet groups that were aggregated to one mixed sample for each species. * indicates significantly different diets. The number of samples refers to the number of pellet groups that were aggregated to one mixed sample for each species.

	No. of samples	Small herbivore sp.	Kob	Hartebeest	Waterbuck	Zebu	Roan	Buffalo	Hippo
Small herbivore sp.	6		0.38*	0.34*	0.67	0.28*	0.40*	0.30*	0.18*
Kob	10	0.08*		0.99	0.91	0.89	0.97	0.99	0.94
Hartebeest	9	0.13*	0.52		0.89	0.92	0.98	0.98	0.94
Waterbuck	5	0.39	0.23	0.31		0.75	0.89	0.84	0.73
Zebu	8	0.03*	0.41	0.32	0.05*		0.95	0.93	0.95
Roan	4	0.12*	0.55	0.59	0.37	0.37		0.96	0.92
Buffalo	5	0.13*	0.39	0.57	0.20	0.59	0.48		0.98
Hippo	11	0.06*	0.46	0.45	0.06*	0.77	0.50	0.75	

Table 3. Resource overlap (expressed as Pianka's index) between species pairs of herbivores at both the food category level (upper right half of matrix) and the grass taxon level (lower left half) in the wet season. For details see Table 1.

	No. of samples	Kob	Hartebeest	Zebu	Roan	Hippo
Kob	9		0.99	0.95	1.00	0.98
Hartebeest	5	0.93		0.93	0.97	0.94
Zebu	9	0.75	0.82		0.95	0.93
Roan	9	0.89	0.91	0.80		0.99
Hippo	10	0.50	0.61	0.50	0.62	

red-flanked duiker) from the dry season analyses does not change this outcome (taxon level: Z = −0.23, P = 0.82, category level: Z = 0.11, P = 0.37). When hippopotamus, the only non-ruminant in this study, is also omitted from the analyses the relation between body mass and diet composition remains non-significant (dry season, taxon level: Z = −0.28, P = 0.73, category level: Z = −0.19, P = 0.59).

The observed dietary overlap in Bénoué NP was significantly greater than the mean overlap of randomized resource use matrices, both in the dry and the wet season, and both at the taxon level and the food category level (all with P < 0.01). As shown by the scatterplots (Figure 3), there appears to be no clear relation between body mass and any of the diet quality parameters. Compared with the faeces of the ruminant species, hippo faeces have relatively low nitrogen and phosphorus concentrations and high fibre concentrations. When all species are considered, significant relationships are found by the Spearman rank correlation analyses between body mass and phosphorus (dry season r = −0.41, P < 0.05; wet season r = −0.70, P < 0.01) or nitrogen (wet season only) (r = −0.10, P < 0.05). No significant relation could be found between body mass and fibre concentrations (dry season NDF r = 0.00, P = 0.85; wet season r = 0.60) or nitrogen in the dry season (r = −0.19, P = 0.10). When the analyses focus on ruminants only (thus leaving out hippo), none

of the relationships was significant in either season (dry season: NDF r = 0.00, P = 0.85, nitrogen r = 0.21, P = 0.93 and phosphorus r = −0.11, P = 0.66; wet season: NDF r = 0.60, P = 0.17, nitrogen r = 0.80, P = 0.12 and phosphorus r = −0.40, P = 0.33).

DISCUSSION

Diet selection and resource partitioning

In contrast to the Jarman–Bell principle and recent data on ungulates in a South African savanna (Codron *et al.* 2007), our data on West African herbivores do not support the hypothesis that smaller herbivores select forage of higher quality than do larger herbivores. However the results of our study support the species richness–niche width theory of MacArthur & Levins (1967). They suggested herbivore species richness to be a function of resource availability and niche relationships among species, but they did not address food quality as a factor determining resource partitioning.

Although there appeared to be negative relationships between body mass and nitrogen or phosphorus in the faeces, most relationships were no longer significant or even turned positive when hippopotamus was left out of the data analyses. In both the dry and the wet season, nitrogen and phosphorus concentrations of hippopotamus faeces were much lower than of the other species. In contrast to antelopes and buffalo (family Bovidae), hippopotamus is a non-ruminating foregut fermenter, and its digestive physiology is characterized by relatively long gut retention times and low dry matter digestibility compared with ruminants (Clauss *et al.* 2004, Schwarm *et al.* 2006). Bacterial fermentation in the very short hindgut of the hippo is low compared to ruminants (Schwarm *et al.* 2003, 2006) and the lower nitrogen concentrations in hippo faeces thus most likely reflect
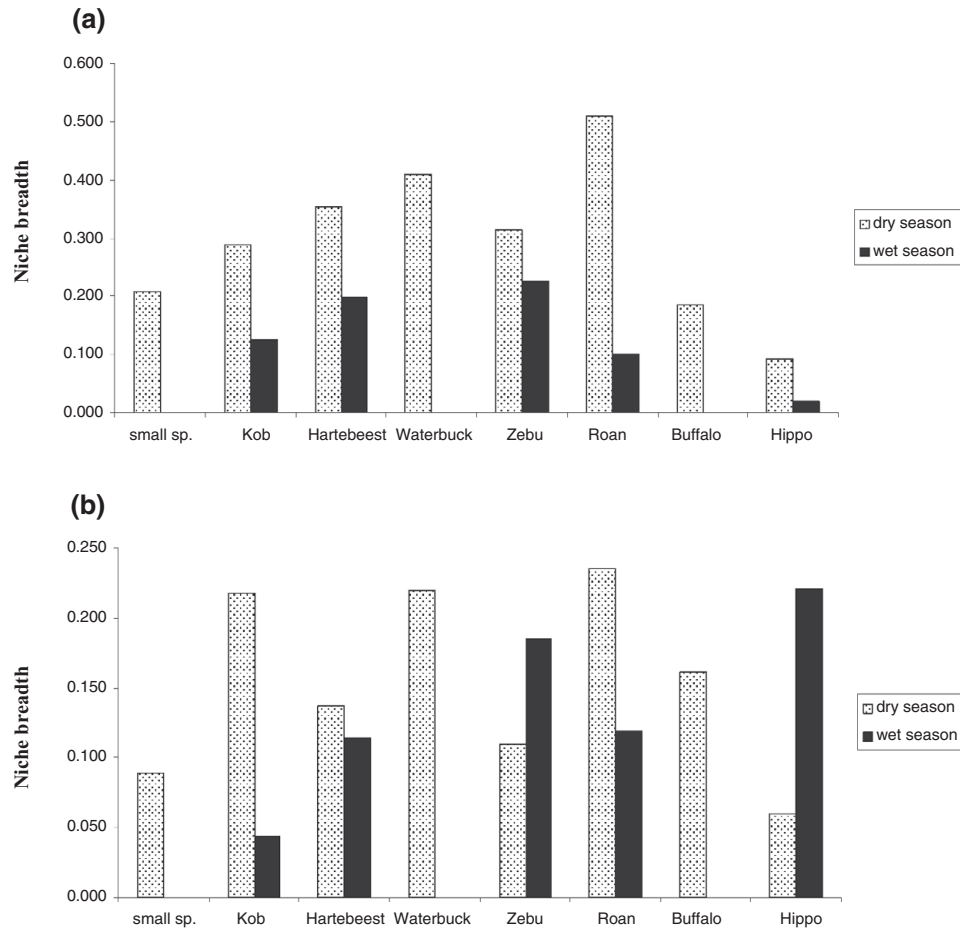
(a)

(b)

Figure 2. Seasonal standardized niche breadth of herbivores in Bénoué N. P., represented by Levins' niche breadth index, standardized to a scale of 0−1 following Hurlbert (1978). Niche breadth for food categories (a), niche breadth for grass species consumed (b).

low losses of bacterial protein rather than a general body mass–diet quality relationship.

Although various studies have argued that fibre digestion increases with body mass (Gordon & Illius 1994, 1996; Iason & Van Wieren 1999, Illius & Gordon 1992, Robbins *et al.* 1995), we could find no clear relation between fibre concentrations and body mass. Likewise, Pérez-Barberia *et al.* (2004) could find no significant effect of body mass of ruminants on fibre digestibility. In spite of an increase in gut capacity in large species compared to small herbivores, gut retention time may be largely independent of body mass in grazing ruminants (Clauss *et al.* 2007) so that a larger body mass does not necessarily lead to improved digestive efficiency. Rather, the digestive efficiency of fibre is more likely to be related to the proportion of grass versus browse in the diet (Pérez-Barberia *et al.* 2004).

In line with previous studies (Codron *et al.* 2007, Mysterud 2000), there appeared to be no effects of body mass on the food plants that were selected. Similar results were reported by Mysterud (2000), who found no

relationship between the degree of diet overlap and body mass among northern European ungulates, and Codron *et al.* (2007), who found no relation between body mass and the proportion of grass in the diet. It should be noted that in our study diet composition does not merely reflect the proportion of grass versus browse, but refers to (1) the grass genera in the diet, and (2) different food categories such as grass stems, fruits, leaves etc. In addition to the above-mentioned studies, Hansen *et al.* (1985) reported no relationship between body mass and dietary diversity of East African ungulates; when re-analysing their data using a Mantel test, no significant correlation can be found between differences in body mass and diet in both the dry ($Z = 0.38$, $P = 0.93$) and the wet season ($Z = 0.19$, $P = 0.76$).

In the dry season the diets of all herbivores, except the unidentified small species, consisted mainly of grasses, followed by old grass stems and sheaths, and the leaves, flower buds and fruits of *Isoberlinia doka*. The latter were consumed in particular by zebu, probably because herdsmen are known to regularly offer lopped branches of
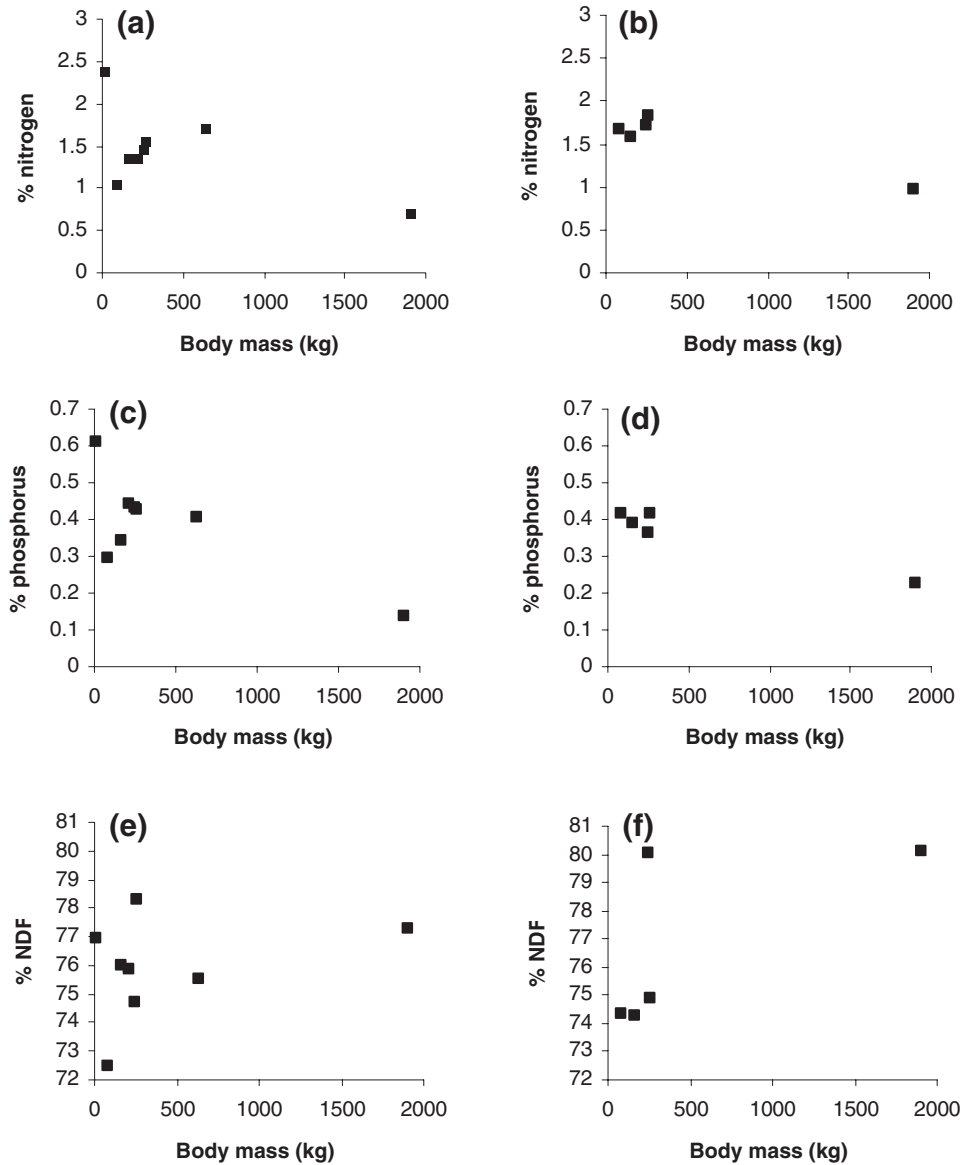
Figure 3. Scatterplots showing the relation between body mass (kg) and faecal nitrogen, phosphorus and neutral detergent fibre (NDF) in the dry (a, c, e) and wet (b, d, f) season.

I. doka trees to their cattle. In the wet season the selection for grasses was much higher, as the diets of all species except zebu cattle consisted of >90% grass. No *I. doka* leaves were consumed in the wet season, although fruits or flower buds of this tree still made up a considerable proportion of the diet of zebu. Although ripe *I. doka* pods are woody, young pods contain pulp (Aubréville 1970, Richter & Cumming 2006) which was found along with pod epidermis. We could not identify any of the seed parts found in the dung. The high proportion of flower buds in the diet of the unidentified small herbivore identifies this species as either common duiker (*Sylvicapra grimmia*) or red-flanked duiker (*Cephalophus rufilatus*).

Comparison of the observed dietary overlap with randomized data showed that the overlap in diet between different herbivore species was much higher than what would be expected on the basis of chance. A high degree of dietary overlap can be interpreted in two different, and exactly opposite, ways (Gotelli & Graves 1996, Mysterud 2000). First, it can mean that competition is intense because species use the same resources. Alternatively, it may indicate that competition is absent, permitting species to share abundant resources (Gordon & Illius 1989, Gotelli & Graves 1996, Mysterud 2000, Putman 1996). The crucial difference is whether or not the shared resources are limiting. Although we did not specifically

test this hypothesis, the generally low animal densities, the seemingly abundant supply of grass and the good physical condition (estimated visually) of herbivores even at the end of the dry season showed no apparent indication of limited resources. In addition, herbivore species in Bénoué NP have been shown to differ in patterns of habitat use and spatial distribution in the burned landscape during the dry season (Klop *et al.* 2007, Mayaka 2002). In this respect it is interesting that Namgail (2009) and Namgail *et al.* (2004) demonstrated that blue sheep (*Pseudois nayaur*) in assemblage with one additional sympatric species, the Ladakh urial (*Ovis vignei vignei*), showed larger niche width and more niche overlap with abundant food resources, compared with a situation with less abundant food resources and two additional sympatric species, feeding on the same resource.

In our study the niche breadth of food categories consumed by five different herbivore species was much lower in the wet season than in the dry season. This was mainly caused by a higher specialization on grasses in the wet season, and lower proportions of old grass stems and other food categories in the wet season diets. The exception to this pattern is zebu cattle, for which differences in diet composition between the dry and wet season are mainly due to changes in the proportions of leaves and flower buds of *Isoberlinia doka* in the diet. However, as mentioned above, this may not be behavioural selection by the animals but the result of what is offered by herdsmen. Patterns in niche breadth for grass genera consumed are slightly different than those for food categories. Kob and roan showed major decreases in niche breadth of grass genera consumed during the wet season compared with the dry season, whereas the niche breadth of zebu and in particular hippopotamus greatly increased in the wet season. The patterns shown by kob and roan can be explained by a strong selection for *Andropogon* species during the wet season, whereas the proportions of different grass species in their dry-season diets were much more balanced. In contrast, in terms of grass genera the wet-season diet of hippopotamus was more balanced than its dry-season diet, and the high proportion of *Elymandra* grasses was no longer visible in the wet season. As is clear from the resource overlap analyses, at the grass taxon level all species showed much higher overlap in the wet season compared with the dry season. This is probably caused by high proportions of *Andropogon* in the wet-season diets of all species, which in the dry season is mostly consumed by hartebeest (which has an index of 12.5% for *Andropogon*, which is between 3.5 to 25 times more than in other species' diets) but not by the other species.

In practice, actual resource competition between large herbivores is difficult to demonstrate, but the presence of overlap in diet (and niche) in combination with similarities in habitat use and spatial distribution, are expected to alleviate competition. However we conclude that in our study area, due to abundant resources and low herbivore densities, especially in the wet season, niche breadth and diet overlap remain large, because there is no need for herbivores to specialize, to avoid competition over scarce resources.

We suggest that, when herbivore densities in our study area would be higher the hypothesis of Gordon & Illius (1996) applies, that large animals may cope with poor-quality diets and thereby avoid competition with smaller species by having a wider resource-tolerance range, especially during limited periods. In our study area, with low herbivore densities and abundant supply of resources, competition seems absent, and all herbivores can optimize diet quality, independent of body size. We conclude that in a situation of abundant resources and low herbivore densities, resource partitioning and niche segregation are ruled by other factors than diet quality and diet composition alone, such as water dependency, presence of predators and human disturbance.

Data considerations

Faecal analyses have been widely used to study herbivore diet composition and quality (Leslie *et al.* 2007). However, as also shown by our study, interspecific differences in food processing or digestive efficiency can lead to major differences in faecal nutrient or fibre concentrations. Several studies have suggested that fibre digestion efficiency increases with the proportion of grass in the diet (Pérez-Barberia *et al.* 2004), and grazer–browser comparisons based on data from faecal analyses should be made with caution (Codron *et al.* 2007). In addition, faecal protein or fibre concentrations can differ significantly between ruminants and non-ruminants due to different digestive strategies (Clauss *et al.* 2007, Schwarm *et al.* 2006).

Epidermis patterns are most specific in leaves where they can be identified down to species or genus. There is a clear distinction between the epidermis patterns of grasses and non-grasses (Metcalfe 1960) but related species cannot always be separated down even to genus as leaf patterns tend to resemble those of related plants. It is not surprising therefore that clusters of look-alikes occur. Usually in those look-alikes the complete leaf pattern is not similar but there are some striking details and as epidermis fragments in herbivore dung were very small (average 0.03 mm^2 except 0.09 mm^2 for hippo) identification may sometimes be doubtful. This was especially the case for the genera *Heteropogon*, *Hyparrhenia* and *Schizachyrium*, all belonging to the same subfamily (Panicoideae), that all show more or less similar papillae and dumbbell-shaped silica cells. Different vein patterns occur in the genera *Aristida*, *Zea*, *Chloris*, *Ctenium*, *Cynodon*, *Dactyloctenium*,

Eleusine, *Eragrostis* or *Sporobolus*, most of them from the subfamily Chloridoideae.

Conclusions

Our data suggest that grazing herbivores in Bénoué NP do not segregate in food quality or diet composition along a body mass axis. The lack of a body mass–diet quality relationship is in sharp contrast to the widely supported Jarman–Bell hypothesis (Bell 1971, Jarman 1974). Although several studies have demonstrated an effect of body mass on diet quality of African ungulates, such as recently by Codron *et al.* (2007), the relation between digestive efficiency and body mass may be questionable (Clauss *et al.* 2007, Pérez-Barberia *et al.* 2004).

As shown here, there can be considerable overlap in the diet composition among mammalian savanna herbivores. The high overlap does not necessarily also imply nutritional overlap since different herbivore species can select post-fire regrowth of different age (Klop *et al.* 2007) and hence, different nutritional quality (Van de Vijver *et al.* 1999). Although our study provides insight into the importance of body mass, diet quality and diet composition on patterns of resource partitioning among West African herbivores in the dry season and early wet season, further research is needed to investigate patterns of resource partitioning deeper into the wet season, when many herbivores graze on the grazing lawns of hippopotamus (Verweij *et al.* 2006) instead of the post-fire regrowth that is abundant in the dry season.

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