

Functional differentiation of African grazing ruminants: an example of specialized adaptations to very small changes in diet

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We assess whether interspecific differences in craniodental morphology within a single ruminant feeding guild, the grazers, represent anatomical adaptations to subtle differences in diet. Differences in craniodental anatomy follow a distinct taxonomic pattern that is paralleled by dietary niche differentiation recorded in species' stable carbon ($\delta^{13}\text{C}$) and nitrogen isotope ($\delta^{15}\text{N}$) compositions, strongly supporting a hypothesis for functional divergence within the grazers. We propose that the evolutionary origin of grazers were multifold; at least two and up to four different types of grazing can be discerned within the 11 taxa studied here alone. However, correspondence between craniodental adaptations and isotopic differences across species are not found when only $\delta^{13}\text{C}$ data are considered (i.e. morphological differences do not reflect varying proportions of C_3 browse to C_4 grass consumed). This implies that alternate anatomical adaptations to grazing are not related to differences between variable (part-time browsing) and obligate grazers, as previously predicted. Rather, anatomical differences correlate strongly with changes in $\delta^{15}\text{N}$, which we infer to reflect functional responses to changes in diet quality associated with the degree of feeding selectivity and short-, medium-, or tall-grass grazing. © 2008 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2008, 94, 755–764.

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INTRODUCTION

Studies of macroevolutionary trends in animals rely heavily on anatomical adaptations to diet (Fortelius, 1985; Langerhans *et al.*, 2003). One group that has contributed substantially to the development of

hypotheses about relationships of form with function are the ruminants. Their exceptional species richness, particularly on the African continent, is attributed primarily to differentiation between two feeding guilds: browsers and grazers (Clauss, Kaiser & Hummel, 2007). Emphasis has been placed on morpho-physiological differences between browsers and grazers, in association with different chemical and

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physical properties of their respective food sources. For example, the coarseness of grass relative to browse is assumed to explain why grazers differ from browsers in having larger enamel crowns (to resist tooth abrasion), wider muzzles (enabling bulk intake), and a number of gastrointestinal specializations that enhance fibre-digestion efficiency (Clauss *et al.*, 2007).

In reality, this dichotomous scheme oversimplifies true functional divergence because there are feeding niche differences within the two guilds. Browsers include folivores and frugivores (Gagnon & Chew, 2000), and their dietary niches also differ with respect to feeding height (du Toit, 2003). In grazers, a succession from tall- to short-grass feeding has been proposed (Bell, 1971), and recent studies advocate the distinction between variable (part-time browsing) and obligate grazers (Gagnon & Chew, 2000; Cerling, Harris & Passey, 2003; Codron, Codron *et al.*, 2007a). Few comparative studies have questioned whether these more subtle differences in feeding style also gave rise to peculiar anatomical specializations, such as differences in face length or muzzle width; those that have are limited to two species (Schuette *et al.*, 1998; Murray & Illius, 2000).

The lack of extensive research in this area is likely because our ability to test hypotheses about intra-guild variations is hampered by difficulties encountered in quantifying feeding habits that differ only at very subtle scales. Stable isotope tools offer a unique approach to herbivore niche differentiation, providing empirical records of dietary continuity and variability (Cerling *et al.*, 2003; Sponheimer *et al.*, 2003a; Codron *et al.*, 2007a). $^{13}\text{C}/^{12}\text{C}$ ratios in body tissues of African savanna herbivores reflect proportions of C_3 (browse) to C_4 (grass) biomass consumed (Cerling & Harris, 1999). $^{15}\text{N}/^{14}\text{N}$ ratios in animal tissues vary with trophic position and with dietary protein levels and quality, although values may also be influenced by climatic and ecophysiological stress conditions (Ambrose, 1991; Sponheimer *et al.*, 2003b; Robbins, Felicetti & Sponheimer, 2005). Used in tandem, herbivore $^{13}\text{C}/^{12}\text{C}$ and $^{15}\text{N}/^{14}\text{N}$ composition records differences in feeding niches even amongst animals that concentrate at the C_3 - or C_4 -end of the continuum (Stewart *et al.*, 2003; Codron & Brink, 2007).

In the present study, we use craniodental parameters in combination with stable carbon and nitrogen isotope evidence to assess relationships between form with dietary niche amongst the grazers, including ten African bovid taxa, and one equid (a hindgut fermenter) as an outgroup.

MATERIAL AND METHODS

Specimens were selected from collections of the Florisbad Quaternary Research Station, Brandfort,

South Africa, using animals that lived in the savanna and grassland biomes of the country's interior (for biome descriptions, see Rutherford & Westfall, 1994). Species included are black wildebeest *Connochaetes gnou*, blue wildebeest *Connochaetes taurinus*, blesbok *Damaliscus pygargus phillipsi*, red hartebeest *Alcelaphus buselaphus*, roan antelope *Hippotragus equinus*, sable antelope *Hippotragus niger*, waterbuck *Kobus ellipsiprymnus*, oryx *Oryx gazella*, reedbuck *Redunca arundinum*, buffalo *Syncerus caffer*, and the equid Burchell's zebra *Equus burchellii*. We measured four craniodental parameters that have been associated with reliance on grass-based diets (Spencer, 1995; Mendoza & Palmqvist, 2006; Clauss *et al.*, 2007) lower (L) and upper (U): premolar : molar row length ratio (LP : M and UP : M row length ratio (lower LP : M); mandibular angle (MA, the angle of orientation between mandible and cranium measured from the posterior extremity of the occlusal surface to the skull articulation); and premaxillary width (PW, reported in relation to the upper premolar plus molar row length (UPML) to control for body size changes) of, where possible, five individuals of each species (Fig. 1). We also determined the hypsodonty index (HI) from depth : width ratio of M_3 enamel crowns, based on computed tomography scans to measure depth within the mandible. For HI, we used only specimens with unworn M_3 crowns, and thus had to settle on only one specimen per species.

Stable isotope data are for tooth dentine collagen of specimens in the Florisbad collections, selecting up to ten individuals per species where available. Dentine powder was drilled from the M_2 or M_3 of selected individuals, representing only adult or sub-adult growth stages. Each sample was treated in 0.2 M HCl solution to isolate the collagen phase of the dentine. Freeze-dried collagen was combusted in an automated Elemental Analyzer (Carlo Erba, Milan), and the resultant CO_2 and N_2 gases introduced to a Finnigan MAT 252 or DELTA XP Mass Spectrometer (Finnigan, Bremen) via a continuous flow-through inlet system. We report $^{13}\text{C}/^{12}\text{C}$ and $^{15}\text{N}/^{14}\text{N}$ ratios in conventional δ notation, in parts per mil (‰), relative to the Vienna PeeDee Belemnite and atmospheric N_2 standards, respectively. Standard deviations of repeated measurements of laboratory standards were less than 0.1‰ for $\delta^{13}\text{C}$ and 0.3‰ for $\delta^{15}\text{N}$.

For some taxa, namely roan and sable antelope, only three and two specimens, respectively, could be located that were suitable for isotope analysis. Thus, we combined our data with previously published results for hair from these ($N = 13$ and $N = 8$, respectively) and other species from similar South African savanna environments (Codron *et al.*, 2007b). On visual inspection, patterns of isotopic separation

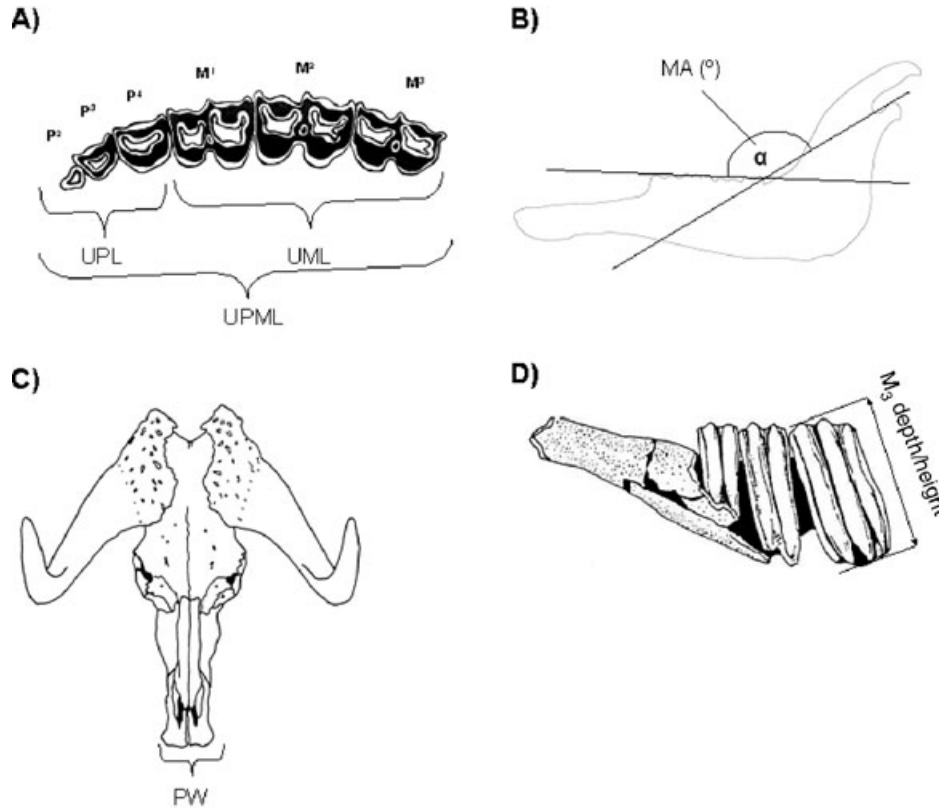


Figure 1. Diagrammatic representation of craniodental measures used in the present study. A, maxillary tooth row; B, mandible; C, cranium; D, exposed M3 crown in the mandible. UPL, upper premolar length (in mm); UML, upper molar length (in mm) (these two reported as P : M length ratios); UPML, total upper tooth row length (in mm); MA, mandibular angle, the effective orientation of the mandible relative to the skull (reported relative to UPML); PW, premaxillary width (in mm). Note that tooth row length measurements (A) were repeated for mandibular teeth as well. Note also that (D) shows an exposed tooth crown of a fossil bovid specimen; for our study of modern animals, crown depth was measured using computed tomography scans because depth in the mandible varies between species, and indeed between individuals of the same species. The hypsodonty index (HI) was calculated from M₃ crown height : width ratios (measured in mm).

between species appear to be similar for the hair and dentine datasets (Fig. 2A,B). For example, the lowest $\delta^{15}\text{N}$ values are recorded for roan antelope, sable antelope, and reedbuck, the highest $\delta^{15}\text{N}$ are found in wildebeest, and, although buffalo have similar $\delta^{15}\text{N}$ compared with the hartebeest/blesbok complex, they have lower $\delta^{13}\text{C}$ values. It was thus considered that combining the two datasets would be an appropriate way to increase sample sizes for under-represented taxa. Because of differences in diet-tissue ^{13}C discrimination between collagen (approximately 4.5‰) and hair (approximately 3.2‰) (Ambrose & Norr, 1993; Cerling & Harris, 1999), we converted hair $\delta^{13}\text{C}$ data to collagen 'equivalents' by adding 1.3‰. Similar 'multi-tissue' approaches have been shown previously to yield satisfactory results (Cerling *et al.*, 2003; Sponheimer *et al.*, 2003a). Indeed, Mann-Whitney *U*-tests revealed that, within each species, collagen and 'converted' hair $\delta^{13}\text{C}$ values were similar

($P = 0.12\text{--}0.79$), as were $\delta^{15}\text{N}$ values of the two tissues ($P = 0.11\text{--}1.00$), indicating that conversions had been successful.

To establish anatomical groupings within grazers, we used cluster analysis based on the Euclidean Distance method, from a data matrix including means for each craniodental parameter per species. We used analysis of variance to test for significant differences between taxa (craniodental and isotopic variables) but, because of the small number of taxa included here ($N = 11$), nonparametric models (Mann-Whitney) are used to test for differences between particular species. Similarly, we used the nonparametric Spearman's rank correlation co-efficient to test for relationships between craniodental and isotopic parameters, repeating the correlation trials with and without the equid. Isotope data are also correlated with body size, based on mean body mass of females reported by Estes (1991).

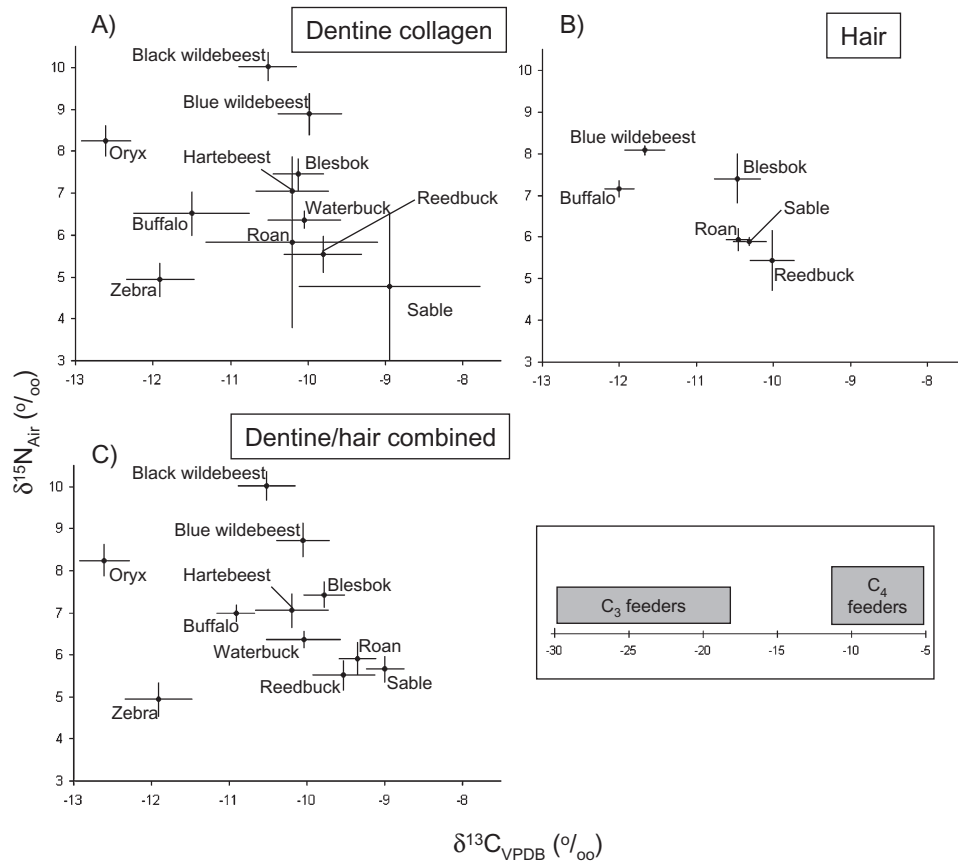


Figure 2. Stable carbon and nitrogen isotope-based differentiation of ecological niches in African grazers. Results are from dentine collagen (A); hair (data from Codron *et al.*, 2007b) (B); and both materials combined (C) after converting hair $\delta^{13}\text{C}$ values to collagen ‘equivalents’ by adding 1.3‰ according to average differences in diet-tissue discrimination between the two tissues (Ambrose & Norr, 1993; Cerling & Harris, 1999). Symbols depict species’ means \pm SE. The inset shows the expected maximum range of $\delta^{13}\text{C}$ values for dentine collagen of herbivores with pure C₃- and pure C₄ diets, respectively.

RESULTS

Craniodental measures differ significantly between bovid species ($P < 0.0001$ for LP : M, UP : M, MA, and PW : UPML; Table 1). Cluster analysis reveals a pattern of species separation reflecting tribal affiliations within the Bovidae (Fig. 3), and the resultant tree diagram separates Alcelaphini from Reduncini and Hippotragini. This separation can be ascribed to the shorter premolar row, steeper orientation of the mandible, wider muzzle, and higher M₃ crown of alcelaphines, which are features most pronounced in black wildebeest. Roan antelope, by contrast, have enlarged premolars, upright mandibles, among the narrowest muzzles, and very low M₃ crowns. Within the alcelaphines, the hartebeest/blesbok complex forms an intermediate group between the wildebeest and other tribes. Oryx (tribe Hippotragini) are an exception. Although oryx have similarly upright mandibles and narrow premaxilla compared with

other hippotragines, this species also shows similarities with the alcelaphines in its somewhat reduced premolar row (Table 1; Fig. 3).

Buffalo also deviate from the general bovid trend in having relatively large premolars but also a broad premaxilla. The zebra has larger premolars, more upright mandibles, and smaller muzzle width compared with overall means for bovinds ($P < 0.01$ in all cases). However, although reductions in the bovid premolar row are associated with increased hypsodonty, zebra have very hypsodont third molars despite their high LP : M and UP : M.

Stable isotope separation of feeding niches, based on analysis of dentine collagen (Fig. 2A), hair (Fig. 2B), and the combined data after adjustments for discrimination (Fig. 2C), follow a similar pattern as revealed from our analysis of craniodental anatomy. First, despite that all taxa are primarily C₄ feeders (mean $\delta^{13}\text{C}$ ranges from -12.1 to -8.5 ‰), there are significant differences in mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$

Table 1. Means and minimum-maximum ranges for craniodental parameters of the 11 grazer species used in the present study

Parameter	Species	N	Mean	Minimum	Maximum	Species	N	Mean	Minimum	Maximum
LP : M	Black wildebeest	5	0.26	0.21	0.35	Waterbuck	6	0.51	0.46	0.59
UP : M		5	0.47	0.31	0.64		5	0.62	0.57	0.68
MA		5	160	159	160		5	150	140	158
PW : UPML		5	0.70	0.62	0.77		5	0.47	0.37	0.53
HI			6.37					3.34		
LP : M	Blue wildebeest	5	0.32	0.24	0.40	Oryx	5	0.58	0.50	0.74
UP : M		5	0.47	0.44	0.51		5	0.49	0.44	0.55
MA		5	158	154	160		5	156	153	161
PW : UPML		5	0.63	0.53	0.79		5	0.47	0.42	0.53
HI			5.57					3.07		
LP : M	Blesbok	5	0.35	0.31	0.38	Reedbuck	5	0.47	0.45	0.54
UP : M		5	0.48	0.36	0.59		5	0.55	0.43	0.66
MA		5	155	152	157		5	151	146	157
PW : UPML		5	0.53	0.45	0.61		5	0.42	0.30	0.51
HI			5.73					3.59		
LP : M	Red hartebeest	5	0.44	0.42	0.47	Buffalo	5	0.59	0.54	0.64
UP : M		5	0.51	0.42	0.59		5	0.69	0.62	0.76
MA		5	154	150	159		5	149	147	151
PW : UPML		5	0.56	0.44	0.68		5	0.66	0.60	0.72
HI			4.80					4.08		
LP : M	Roan antelope	3	0.67	0.64	0.71	Burchell's zebra	5	1.07	0.92	1.19
UP : M		4	0.76	0.65	0.85		5	1.29	1.19	1.38
MA		3	147	144	152		5	147	142	150
PW : UPML		4	0.45	0.39	0.51		5	0.39	0.36	0.44
HI			2.96					5.81		
LP : M	Sable antelope	3	0.60	0.54	0.67					
UP : M		5	0.65	0.60	0.72					
MA		2	149	145	152					
PW : UPML		3	0.55	0.49	0.58					
HI			<i>n.d.</i>							

HI, hypsodonty index (M_3 enamel crown height : width ratio); LP : M, lower premolar to molar row length ratio; MA, mandibular angle; PW : UPML, premaxillary width : upper premolar and molar row length; UP : M, upper premolar : molar row length ratio.

between species ($P < 0.0001$ for both parameters). The most obvious differences are in mean $\delta^{15}\text{N}$ values, which are highest in wildebeest and lowest in the reduncines and hippotragines ($P < 0.01$). Wildebeest also have higher mean $\delta^{15}\text{N}$ compared with alcelaphines of the hartebeest complex ($P < 0.05$). Oryx differ from other hippotragine taxa, having lower $\delta^{13}\text{C}$ than both *Hippotragus* spp. ($P < 0.001$), consistent with greater consumption of C_3 foods, and also have higher $\delta^{15}\text{N}$ ($P < 0.01$), indeed, as high as that in wildebeest ($P = 0.46$). Buffalo are the only bovid besides oryx to have $\delta^{13}\text{C}$ below -10% ($P < 0.01$ com-

pared with other bovids). For zebra, mean $\delta^{13}\text{C}$ is lower than that of all the bovids besides oryx ($P < 0.001$), and $\delta^{15}\text{N}$ is as low as recorded for *Hippotragus* spp.

By contrast to most predictions, no significant correlation between $\delta^{13}\text{C}$ and craniodental anatomy could be found (Fig. 4A–E). Conversely, we find exceptionally strong correlations of anatomy with $\delta^{15}\text{N}$: increasing $\delta^{15}\text{N}$ values with reductions in the premolar row (lower $R = -0.75$, $P < 0.01$; upper $R = -0.85$, $P < 0.001$), a steeper mandibular angle ($R = 0.89$, $P < 0.001$) and wider premaxilla ($R = 0.71$, $P < 0.05$;

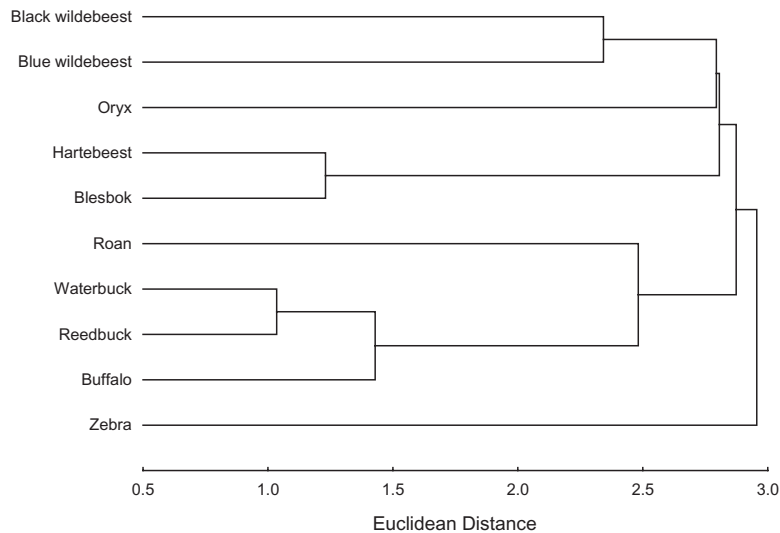


Figure 3. Tree diagram representing cluster analysis using the Euclidean Distance matrix of means of all five craniodental parameters measured. Note that sable antelope are excluded from the analysis because the hypsodonty index was not measured for this species.

Fig. 5A–D). The strength of these correlations persists even when the zebra are excluded ($R = -0.68$, $P < 0.05$; $R = -0.81$, $P < 0.01$; $R = 0.85$, $P < 0.01$; $R = 0.61$, $P = 0.06$, respectively). With the zebra removed, there appears to be a trend of increasing HI with increasing $\delta^{15}\text{N}$ ($R = 0.65$, $P = 0.06$; Fig. 5E). There are no significant correlations between either $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ with body mass in these taxa (Figs 4F, 5F).

DISCUSSION

The parallels in craniodental and isotopic distributions between taxa strongly support the hypothesis that taxonomic diversification within these grazers followed the differentiation in ecological niche. The most obvious trends are differences in anatomy and isotope-based feeding niches between wildebeest, hartebeest, and reduncines/hippotragines. The craniodental anatomy of buffalo, and indeed zebra, places them apart from the other species we studied, as do their carbon and nitrogen isotopic compositions. It has been proposed that herbivore taxonomy and functional morphology are only incidentally correlated (Stucky, 1990). Several cases in the present study support this argument. First, similarities between reduncines and hippotragines, which, based on molecular evidence, do not share similar phylogenetic histories (Gatesy *et al.*, 1997), imply that parallel ecological and adaptive changes occurred rather than inherent genotypic forcing of tooth morphology through time. Second, the oryx, a hippotragine, clusters towards the alcelaphines, both anatomically and

isotopically, implying some degree of convergence on the alcelaphine niche, especially wildebeest. Our study concurs with the hypothesis of Jernvall, Hunter & Fortelius (1996), who proposed that, because morphological evolution occurs more rapidly than speciation and taxonomic turnover, the variety of diets and ecological niches that occur within ungulate herbivores exceeds even their species richness.

All this means that past radiation(s) within the grazers can be traced to subtle differences in their dietary niches, but less so to phylogenetic affiliations. Yet there appears to be no split between grazer feeding styles. Our carbon isotope data show that very little, if any, of the variety of craniodental morphologies observed across grazer species can be associated with changes between obligate and part-time browsing. Although this result may be an artefact of the very small differences in mean $\delta^{13}\text{C}$ (often less than 1‰) between species, there were distinct clusters in $\delta^{13}\text{C}$ distributions, most notably between the alcelaphines and *Hippotragus* spp. Codron *et al.* (2007a) pointed out that the species composition of proposed ‘obligate’ and ‘variable’ grazer types is variable between habitats, and hence likely to be redundant. By contrast, the exceptional strength of relationships between $\delta^{15}\text{N}$ with craniodental anatomy were unexpected, and warrant further investigation.

It is possible that $\delta^{15}\text{N}$ changes between species are the result of different ecophysiological responses to environmental stress factors (Ambrose, 1991). The low $\delta^{15}\text{N}$ of zebra might be related to absence of urea-recycling mechanisms in hindgut-fermenters, which, in ruminants, have been proposed to effect

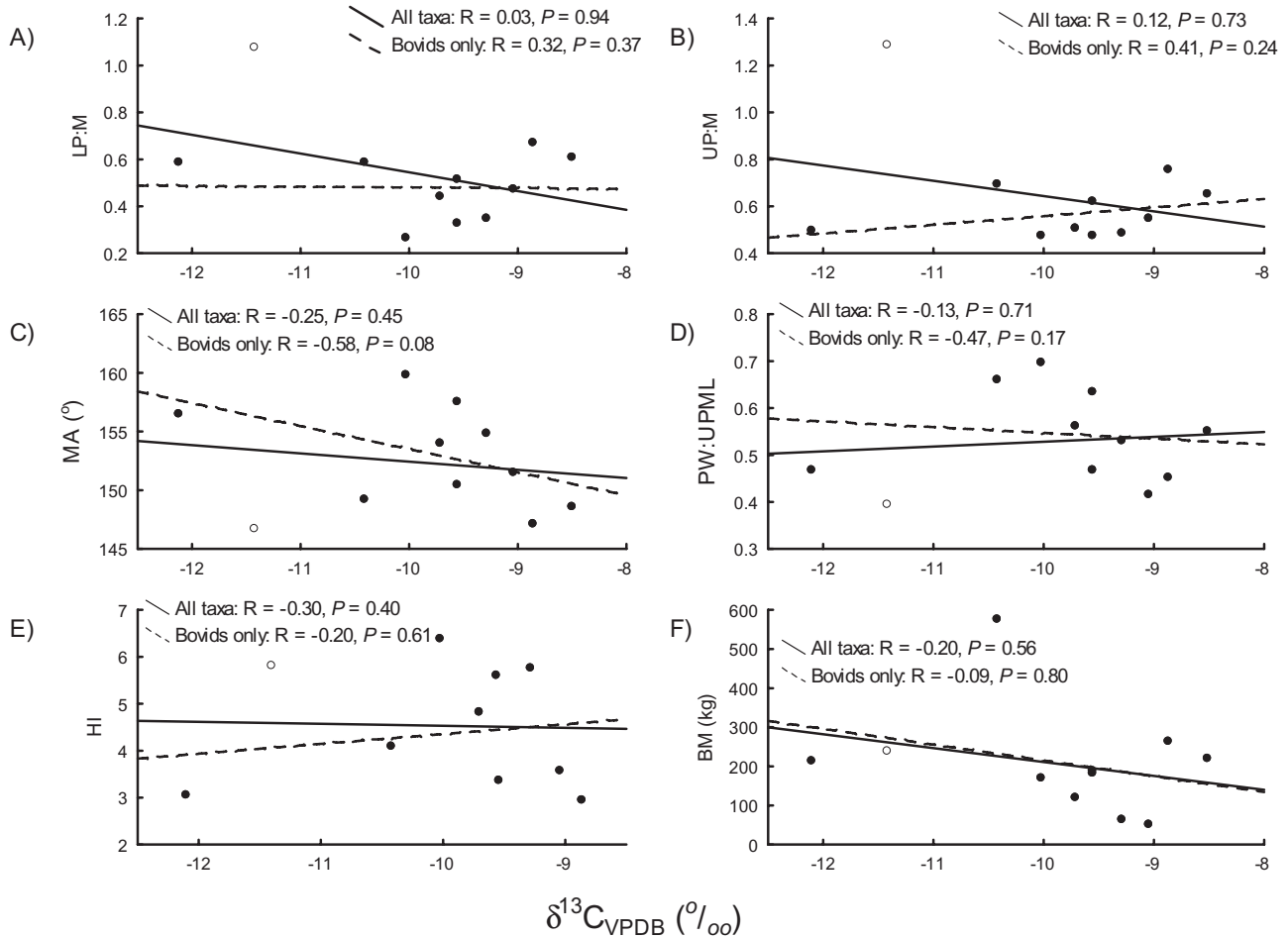


Figure 4. Spearman's rank correlation co-efficients for relationships of $\delta^{13}\text{C}$ in grazers with craniodental anatomy. Morphological characters are A, lower premolar length ratio, LP : M; B, upper premolar : molar length ratio, UP : M; C, mandibular angle of orientation relative to cranial attachment, MA; D, premaxillary width to upper cheek tooth length ratio, PW : UPML; E, hypsodonty index, HI, calculated as M_3 enamel crown height : width ratio; and F, body mass, BM, reported as mean BM of females (data from Estes 1991). Symbols depict means for each species; closed symbols represent bovinds and open circles zebra. Analyses are repeated across all taxa (solid fit-lines) and within bovinds only (hashed fit-lines).

internal microbial trophic contributions leading to elevated $\delta^{15}\text{N}$ (Sponheimer *et al.*, 2003b). However, recent studies have revealed that such ecophysiological effects are negligible in comparison with positive ^{15}N -feedback mechanisms associated with increased dietary protein levels or, more specifically, increases in the biological value of these proteins (Sponheimer *et al.*, 2003b; Robbins *et al.*, 2005). Increased $\delta^{15}\text{N}$ with increasing dietary protein levels (faecal %N) has also been reported in free-ranging situations for southern African ungulates at inter- and intra-specific levels (Codron *et al.*, 2005a; Codron & Brink, 2007). Thus, the most likely explanation is that $\delta^{15}\text{N}$ patterns reveal anatomical adaptations to diet quality, with elevated $\delta^{15}\text{N}$ reflecting consumption of proteins having greater metabolic value (Robbins *et al.*, 2005).

Complementary to this is that variations in the nitrogen isotope composition of plant foods have also been shown to have greater influence for herbivore $\delta^{15}\text{N}$ than physiological responses to water stress (Murphy & Bowman, 2006). In the context of the present study, changes in grazer $\delta^{15}\text{N}$ could reflect differences in preferred grass types eaten; higher $\delta^{15}\text{N}$ values occur in higher quality (high protein/low fibre), often short, grasses of the NAD-malic enzyme and PCK photosynthetic sub-types (chloridoids and panicoids), whereas lower values characterize poorer quality, taller NADP-malic enzyme grass types (andropogonoids) (Codron *et al.*, 2005b); see also (Sage, Li & Monson, 1999).

Based on this interpretation, the nitrogen isotopic trends shown in Figure 5 offer some of the most

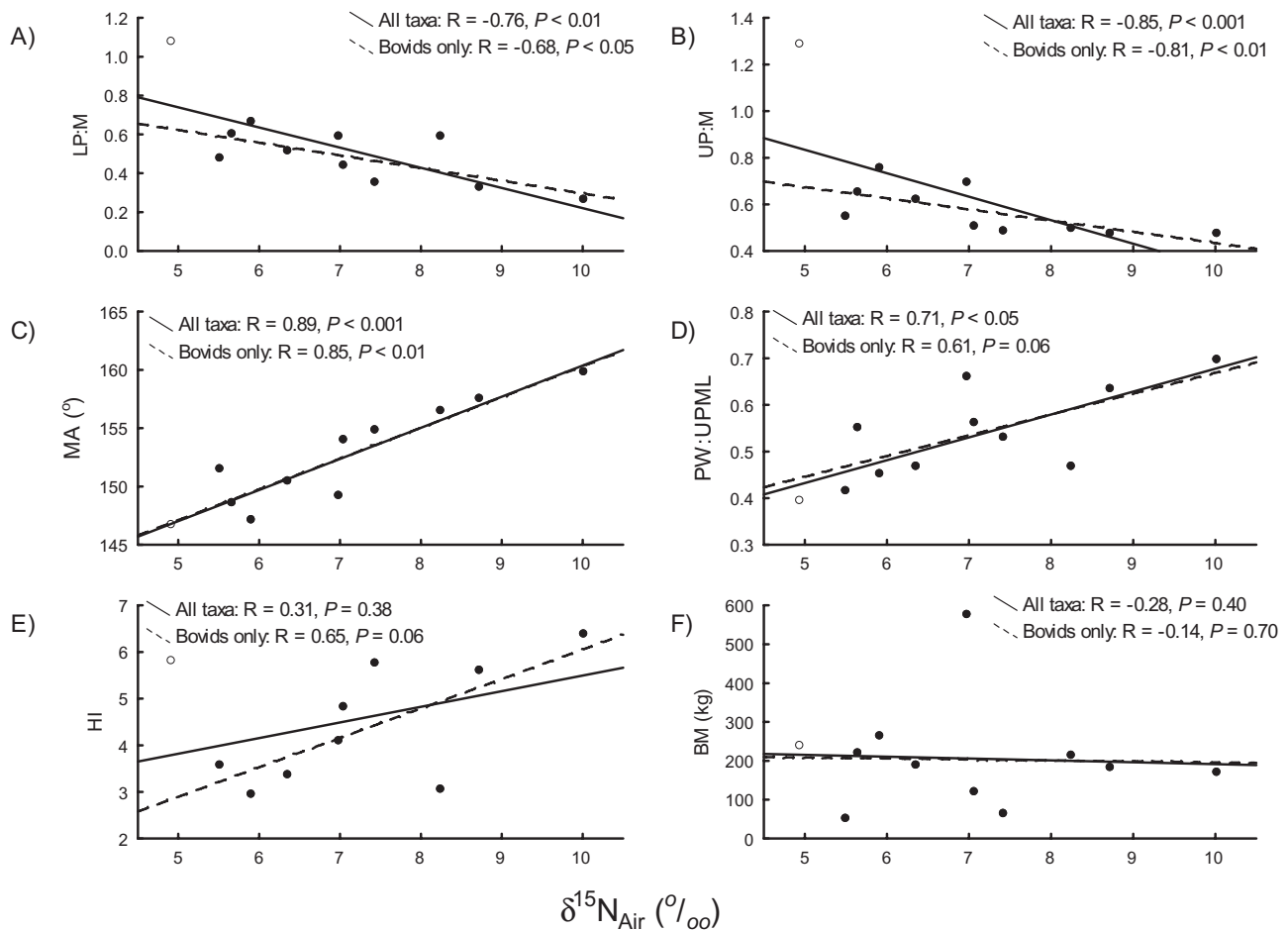


Figure 5. Spearman's rank correlation co-efficients for relationships of $\delta^{15}\text{N}$ in grazers with craniodental anatomy. Morphological characters are A, lower premolar : molar length ratio, LP : M; B, upper premolar : molar length ratio, UP : M; C, mandibular angle of orientation relative to cranial attachment, MA; D, premaxillary width to upper cheek tooth length ratio, PW : UPML; E, hypsodonty index, HI, calculated as M_3 enamel crown height : width ratio; and F, body mass, BM, reported as mean BM of females (data from Estes 1991). Symbols depict means for each species; closed symbols represent bovids and open circles zebra. Analyses are repeated across all taxa (solid fit-lines) and within bovids only (hashed fit-lines).

conclusive evidence for functional differentiation within the grazing guild to date, and from which we can deduce two main routes in the evolutionary diversification of grazing, based primarily on relative degrees of diet selectivity. The first is consistent with common predictions for a reduced premolar row, higher M_3 enamel crown, and more acute orientation of the mandible relative to the skull (i.e. emphasis on comminution towards the back of the jaw) (Spencer, 1995; Mendoza & Palmqvist, 2006). These adaptations occur in high quality short/medium-grass grazers (hartebeest complex) and are most extreme in short-grass grazers (wildebeest), accompanied, especially in the latter, by a broader muzzle width enabling ground-level feeding (Bell, 1971; Murray & Illius, 2000). A wider premaxilla also facilitates larger

bite size, which, coupled with a reduced premolar row, explains the emphasis on posterior jaw mechanics. The reduced premolar row reduces the arm of momentum of the mandibular joint and thus reduces mechanical stress that would be caused by rostral processing of large volumes ingested per unit time (Greaves, 1991). Hypsodonty is predicted to be an adaptation to resist tooth wear by coarse foods, reflected largely in the amount of abrasive grit ingested (Janis, 1988; Sanson, Kerr & Gross, 2007). Increasing the M_3 enamel crown height thus acts to resist tooth wear induced by high quantities of grit ingested during ground-level feeding. Oryx, with higher $\delta^{15}\text{N}$ and more reduced premolar row compared with other hippotragines, may form part of this group but the significant C_3 component of their diets,

coupled with a low HI, makes it unclear whether part-time browsing or foraging for subterranean items such as roots and tubers (Skinner & Smithers, 1990) had a greater role in their differentiation.

The second route to grazing entails use of relatively large premolars and a more vertical mandible (i.e. dispersing emphasis of mastication throughout the oral cavity). This group exploits taller, coarser grasses with lower nutritional value, and thus cannot merely subsist on bulk intake (i.e. they should be more selective so as to exclude the lowest quality items within this niche). Accordingly, they have narrower muzzles than the alcelaphines implying greater manoeuvrability and smaller bite size. The most extreme case is the roan antelope, a species known to consistently crop grass at higher levels (Gureja & Owen-Smith, 2002). The greatly enlarged premolars and near-vertical mandibular orientation of roan antelope parallels these craniodental adaptations in zebra, and might indicate similar low quality diets as expected for hindgut-fermenters (Duncan *et al.*, 1990). Feeding at higher levels from the ground also means lower quantities of grit are ingested; hence, tall-grass grazers lack the extremely hypsodont M_3 of the alcelaphines.

Buffalo could represent a third grazing type, with relatively wide muzzle and pronounced premolars, adaptations that likely facilitate the ability to consume both short/fresh and tall/coarse grass types (Skinner & Smithers, 1990; Macandza, Owen-Smith & Cross, 2004), as reflected in their intermediate $\delta^{15}N$ values. Hindgut-fermenters (e.g. zebra) contrast with bovids in having extremely hypsodont molars and very large premolars. Zebra need to resist tooth abrasion due to the extreme quantities of food consumed (Bell, 1971; Duncan *et al.*, 1990), their ability to subsist on medium-to-tall grass types (Gureja & Owen-Smith, 2002), and their comparatively longer lifespan.

Classic descriptions of grazers as a monotypic feeding guild are clearly over-simplified. It is unclear whether tribes such as the Reduncini and Hippotragini have simply retained the plesiomorphic conditions observed in browsers, or whether enlargement of the premolar row and the upright orientation of the skull were acquired independently. Given that any evolutionary transition from a plesiomorphic browsing condition to grazing would have incurred enormous morphophysiological investment, and that at least hippotragines are likely a derived branch of the alcelaphine lineage, the latter could have occurred. Under the scenario of grazing forms evolving independently, each group/lineage would have adopted a different strategy to solve a similar ecological problem. Multiple transitions from browsing to grazing have already been documented from carbon isotope studies of fossils in taxa as different as equids,

suids, elephantids, sivatheres and bovids (Cerling, Harris & Leakey, 2005; Codron *et al.*, 2008). We predict that similar multiplicity likely occurred within bovid/tribal lineages.

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