Open access • Journal Article • DOI:10.1139/Z10-077

Rumen physiology constrains diet niche: linking digestive physiology and food selection across wild ruminant species — Source link

Daryl Codron, Daryl Codron, Marcus Clauss, Marcus Clauss

Institutions: University of KwaZulu-Natal, University of Zurich

Published on: 02 Nov 2010 - Canadian Journal of Zoology (National Research Council of Canada)

Topics: Ecological niche

Year: 2010

Rumen physiology constrains diet niche: linking digestive physiology and food selection across wild ruminant species

Codron, D; Clauss, M

Codron, D; Clauss, M (2010). Rumen physiology constrains diet niche: linking digestive physiology and food selection across wild ruminant species. Canadian Journal of Zoology, 88:1129-1138.
Postprint available at:
http://www.zora.uzh.ch

Originally published at:
Canadian Journal of Zoology 2010, 88:1129-1138.

Rumen physiology constrains diet niche: linking digestive physiology and food selection across wild ruminant species

Daryl Codron*[1,2,3], Marcus Clauss[1]

[1]Clinic for Zoo Animals, Exotic Pets and Wildlife, Vetsuisse Faculty, University of Zurich, Winterthurerstr. 260,CH-8057 Zurich, Switzerland

[2]School of Biological and Conservation Sciences, University of KwaZulu-Natal, Private Bag X01, Scottsville, 3209, South Africa

[3]Florisbad Quaternary Research, National Museum, Bloemfontein, 9300, South Africa

* Corresponding author: Clinic for Zoo Animals, Exotic Pets and Wildlife, Vetsuisse Faculty, University of Zurich, Winterthurerstr. 260, 8057 Zurich, Switzerland.

dcodron@vetclinics.uzh.ch; darylcodron@gmail.com

Rumen physiology constrains diet niche: linking digestive physiology and food selection across wild ruminant species

Daryl Codron, Marcus Clauss

Abstract

We propose a hypothesis for digestive constraints on the browsing and grazing options available to ruminants: that the diet niche range (maximum and minimum grass intake) of a species is dependent upon its predisposition to a stratified rumen contents, based on observations that this characteristic is a critical step towards enhanced fibre digestion and greater fluid throughput. We compare a physiological (heterogeneity of ingesta fluid content) and an anatomical (the intraruminal papillation pattern) measure with dietary evidence for a range of African and temperate species. Both measures are strongly related to the mean % grass in species' natural diets, as well as to the maximum and minimum levels of grass intake, respectively. The nature of these effects implies a stratification level threshold, below which a species will not use a grass-based diet, but above which grass consumption can increase exponentially. However, above this threshold, a minimum % grass in the diet is a prerequisite for optimal performance. We argue that this second constraint is crucial, as it depicts how a greater fluid throughput reduces potential for detoxification of plant secondary compounds, and therefore limits the maximum amount of browse a stratifying species will consume.

Keywords: Browsing; Carbon isotopes; Grazing; Rumen papillation; Rumen dry matter; Stratification

Introduction

Ruminants are peculiar amongst herbivores, not only because of their unique digestive systems, but also in the degree of anatomical and physiological convergence across species sharing similar diet niches. At a broad, heuristic, but functionally realistic, scale, their diet niches can be described as being either browse- or grass-based. Differences in digestive morphology across these feeding styles were first described by Hoffman (1973). Since then, numerous morphophysiological differences have been detailed across a wide range of species (reviewed in Clauss et al. 2008*b*), and by now distinction can almost certainly be made between two anatomical prototypes termed “moose-type” and “cattle-type”, respectively (Clauss et al. 2010*b*). These terms are largely concordant with the more traditional terms “browser” and “grazer”, respectively, but refer specifically to morphophysiological design, upon which diet composition is at least partially dependent (Owen-Smith 1982; Clauss et al. 2003; Lechner et al. 2010).

One of the most consistent traits differentiating moose- from cattle-type ruminants is the stratification of rumen contents. The rumen contents of moose-type species are homogeneous, whereas in cattle-type species they are separated into a dorsal gas dome overlaying a fibrous raft, a fluid layer below, and ‘sludge’ formed by very dense particles in the most ventral strata (Hofmann 1973). Differences in stratification between species have been demonstrated based on investigations on passage kinetics of fluids and particles in the reticulorumen (Hummel et al. 2005; Clauss et al. 2006*b*; Lechner et al. 2010), physical characteristics of rumen contents (Clauss et al. 2009*a*; Clauss et al. 2009*b*; Hummel et al. 2009), or by ultrasonographic investigations (Tschuor and Clauss 2008). Several anatomical features appear to reflect differences in stratification across species, notably the papillation pattern of the rumen wall. Whereas surface papillae are evenly distributed throughout the rumen wall in moose-type species, cattle-type species show a consistent reduction of surface papillae in the dorsal and ventral rumen wall, relative to the atrium (Hofmann 1973; Clauss et al. 2009*a*; 2009*b*). The heterogeneous papillation pattern of the cattle-type rumen probably reflects the absence of volatile fatty acids (VFAs) in the gas dome of the dorsal rumen, and sludge layer of the ventral rumen, since VFAs are known to stimulate papillae development (Sakata and Tamate 1978; 1979).

Differences in stratification are expected to have ecological significance for ruminants because they might constrain a species to a browsing or grazing (or mixed-feeding) niche (Owen-Smith 1982; Clauss et al. 2003; Lechner et al. 2010). Early research revealed that the presence of a heterogeneous papillation pattern was typical of grazing species (Hofmann 1973; Owen-Smith 1982; Hofmann 1989). Indeed, stratification has long been accepted as a mechanism for increased particle retention (and hence more efficient digestion of dietary fibre that would benefit species feeding on grass) in the rumen of domestic taxa (Lechner-Doll et al. 1991; Hristov et al. 2003). Several anatomical traits associated with stratification, including the papillation gradient, showed significant correlations with the percent grass composition of species' natural diets (Clauss et al. 2003; Clauss et al. 2009*c*). Thus, the papillation gradient in cattle-type species was interpreted as the consequence of adaptations to a grazing niche, adaptations that would have lead to elevated fluid throughput through the rumen, with the resulting benefits of an increased microbial protein harvest and formation of a fibre raft that aids in particle retention (Clauss et al. 2010*b*). The absence of a papillation gradient in moose-type species was interpreted as the consequence of a viscous proteinaceous saliva functioning as defense against secondary plant compounds common in browse forages (Clauss et al. 2010*b*). However, these interpretations are largely contingent on whether anatomical traits are reliable proxies for stratification, but such systematic associations between anatomy and physiology have rarely been demonstrated. Two recent studies did demonstrate a more heterogeneous rumen fluid content in species that habitually feed on grass compared to browsing species, but included only a small number of taxa (Clauss et al. 2009*a*; Clauss et al. 2009*b*).

In this study we explore how rumen physiology, in particular the predisposition for a stratified rumen content, could influence the facultative range of diet options available to, and used by, ruminant species. We hypothesized that differences in average grass composition in the natural diet closely reflects differences in stratification across species, and that the level of stratification also defines the greater (maximum) and lesser (minimum) levels of grass eaten. We test these predictions using new and previously published data (Clauss et al. 2009*a*; Clauss et al. 2009*b*) on variations in dry matter (DM) concentrations of ingesta within the rumen of shot animals: in fistulated cattle (*Bos taurus* L., 1758), this measure, more than differences in flotation characteristics and particles sizes, could be consistently demonstrated irrespective of diet and time since feeding (Hummel et al. 2009), and thus represents species-specific stratification trends. We compare these data with the anatomical papillation patterns of the species in our sample (Clauss et al. 2009*c*), and with their diet compositions as reported in the literature or inferred from stable carbon isotope analysis of body tissues of the shot animals.

Methods

Data Collection

We determined DM concentrations in the dorsal and ventral rumen contents of six African ruminant species from the Soetdoring and Tussen-die-Riviere Nature Reserves in the Free State Province, South Africa. The region forms part of the grassland biome of the central interior of the country (Rutherford and Westfall 1994), typified by sandy, open grassland habitats that are largely treeless except along river courses. In our sample, four species are grazers (average diet includes >80% grass: red hartebeest *Alcelaphus buselaphus* (Pallas, 1766), *n* = 2, blesbok *Damaliscus pygargus phillipsi* (Pallas, 1767), *n* = 6, black wildebeest *Connochaetes gnou* (Zimmerman, 1780), *n* = 5, and gemsbok *Oryx gazella* (L., 1758), *n* = 4), one species is a mixed-feeder (springbok *Antidorcas marsupialis* (Zimmerman, 1780), *n* = 10), and one a browser (average diet includes <20% grass: greater kudu *Tragelaphus strepsiceros* (Pallas, 1766), *n* = 3). All animals had been shot during routine hunting programs of Free State Nature Conservation in 2007. Rumen contents were sampled following protocols applied in the previous studies (Clauss et al. 2009*a*; 2009*b*).

Samples were placed into plastic bags and stored frozen until dry matter analysis, i.e. drying samples at 103°C for 24 hours to constant weight. We then combined these data with published data for temperate zone ruminants, including one grazer (American bison *Bison bison* (L., 1758), *n* = 10, Clauss et al. 2009*b*), two mixed-feeders (and mouflon *Ovis ammon musimon* (L., 1758), *n* = 19, Clauss et al. 2009*a*; red deer *Cervus elaphus* L., 1758, *n* = 17, Clauss et al. 2009*b*), and two browsers (moose *Alces alces* (L., 1758), *n* = 17, and roe deer *Capreolus capreolus* (L., 1758), *n* = 23; Clauss et al. 2009*a*). Stratification was determined as the arithmetic difference in DM concentration between dorsal and ventral rumen content of each individual.

Anatomical stratification of the rumen was quantified by the surface enlargement factor (SEF) of the dorsal rumen, expressed as a percentage of the SEF of the atrium. This relative dorsal rumen SEF provides a measure of stratification because it reflects the difference in papillation between the dorsal rumen and the site of maximum papillation (data from Clauss et al. 2009*c*, and references therein).

Data for the diets of temperate zone species were taken from the literature, averaging results from a variety of studies that included % grass in the natural diet (see supplementary material). For African species, however, more reliable and scale-specific data are available in the form of stable carbon isotope compositions of body tissues of the same individuals as sampled for rumen content. These data provide a proxy for % grass in the diet, because they reflect relative proportions of C_3 (browse) and C_4 (grass) biomass consumed (Vogel 1978; Lee-Thorp and van der Merwe 1987; Cerling and Harris 1999). We sampled a fragment of the rumen epithelium from each individual, which was later cleaned, freeze-dried, and analyzed for $^{13}C/^{12}C$ composition on a Delta XP Mass Spectrometer (Finnigan, Bremen, Germany). Each sample was combusted in an automated elemental analyzer (Carlo Erba, Milan, Italy), and CO_2 gas was introduced to the Mass Spectrometer via a continuous inlet system. Stable carbon isotope ratios are reported in *per mil* (‰) relative to the Vienna PeeDee Belemnite Standard (VPBD) using delta (δ) notation. The standard deviation of replicate analyses of internal laboratory standards was less than 0.05 ‰. A linear two-source mixing model was used to convert $\delta^{13}C$ values to estimates of percent C_4 (grass) in the diet. We assumed globally-averaged C_3 and C_4 endpoint values of -27.0 and -12.5 ‰, respectively (Cerling and Harris 1999), and a diet-tissue enrichment factor of 1.5 ‰ as reported for muscle tissue in alpaca *Llama pacos* (L., 1758) (Sponheimer et al. 2006).

Statistical Analysis

Hypotheses were tested using simple linear and nonlinear regression (Nonlinear Estimation module of Statistica V8; Statsoft_Inc 2007) analysis of relationships between physiological (differences in dorsal and ventral rumen DM concentrations) and anatomical (relative $SEF_{\text{dorsal rumen}}$) stratification measures, and between both datasets with species' diets. To investigate effects of stratification on diet, we used the mean, as well as the maximum and minimum, percent grass in the diet of each species. We then extended these analyses to a larger dataset of 59 taxa (SEF data only; see Clauss et al. 2009*c*). In all cases, we fitted a variety of linear and non-linear equations to the data, and selected best-fit models based on lowest residual variance and highest R^2, with the criterion that slopes converged on estimates that differed significantly from zero at 95% confidence. Residuals were consistently homogeneous. Models yielding non-normally distributed residuals (Shapiro-Wilks Test) were discarded. Depending on the data, selected models were either linear, exponential ($y = ae^{bx}$), or logarithmic ($y = a + b.\log(x + 1)$).We then explored the predictive capacity of these relationships by comparing predicted grass intake for impala *Aepyceros melampus* (Lichtenstein, 1812) (based on reported dry and wet season relative $\text{SEF}_{\text{dorsal rumen}}$ of this, and model parameters derived in this study) with an independent dataset of its dietary variations in nature. Comparative data are from carbon isotope analysis of faeces from Kruger National Park, South Africa, representing five southern African savanna habitat types over a full year at monthly intervals (Codron et al. 2006).

To control for potential phylogenetic effects, we conducted independent contrasts analysis, based on the phylogeny proposed by Bininda-Emonds et al. (2007). The tree and data matrix were input into the Phylogenetic Diversity Analysis Program (PDAP) for Mesquite Ver. 2.5 (Midford et al. 2003; Maddison and Maddison 2008). Analysis of independent contrasts are not suitable for nonlinear effects (Quader et al. 2004), thus data for the PDAP matrix was $\log_e$-transformed prior to phylogenetic analysis. Branch lengths were transformed using Grafen’s Rho transformation, and relationships between contrasts evaluated by linear least squares regression through the origin.

Often the types of analyses we used would also require controlling for effects of body mass on morphology, physiology, and even diet, using, for example, ANCOVA or multiple regression models. However, there were no significant effects of body mass on either measure of stratification, nor on diet (see Table 1). Thus, there seemed no reason to include body mass as a covariate in our analyses.

Results

Rumen stratification patterns

With regards to DM concentrations of rumen content, the prediction was that, as in other ruminants, ventral rumen contents of the new taxa sampled for this study should be more moist than dorsal rumen contents, especially amongst primarily grazing taxa. In most individuals, a greater DM concentration was found in dorsal compared with ventral rumen content (see supplementary material), although the sample is too small to make reliable pairwise statistical comparisons. Nonetheless, the mean difference between DM concentrations of the dorsal and ventral rumen content of each species was similar to that reported for temperate zone ruminants (Fig. 1), and two-way ANOVA revealed no significant differences between new and previously published data ($F_{1,\,112} = 0.569$; $p = 0.45$). In the combined dataset, there was an effect of feeding style on DM differences ($F_{2,\,112} = 13.074$; $p < 0.0001$), with grazers having greater mean differences than mixed-feeders and browsers (Bonferonni-adjusted *post hoc* test; $p < 0.0001$); this pattern was consistent between the two datasets (interaction $p = 0.82$).

Intraruminal papillation as an anatomical proxy for stratification

The rumen papillation pattern (relative $\mathrm{SEF}_{\mathrm{dorsal\ rumen}}$) closely reflected differences in content stratification across the 11 species for which $\mathrm{DM}_{\mathrm{rumen\ content}}$ data are available ($R^2 = 0.71$, $p < 0.001$; Fig. 2a), even after accounting for phylogeny ($R^2 = 0.80$, $p < 0.001$; Table 1).

Species diets

Stable carbon isotope data for the African specimens were congruent with previously published data for δ^{13}C values of other tissues of these and related taxa from the central interior, and from elsewhere in southern Africa (Sponheimer 2003; Codron et al. 2007*a*; Codron et al. 2008), and with dietary predictions of the literature (e.g. Gagnon and Chew

2000; but see Codron et al. 2007*a*) as reflected by results of the mixing model (see supplementary material).

Relationships between stratification and diet

The mean % grass in species' diets increased consistently with an increase in ingesta stratification across species ($R^2 = 0.93$, $p < 0.0001$; Fig. 3a). The maximum % grass eaten also showed a significant, but slightly weaker, response to increases in stratification ($R^2 = 0.78$, $p < 0.0001$; Fig. 3b), but the minimum % grass intake was again very strongly dependent on stratification ($R^2 = 0.91$, $p < 0.0001$; Fig. 3c). The differences in strengths of these effects are also indicated by differences in their respective slopes (Table 1), but note that while the mean and maximum % grass intake were nonlinearly related to stratification, the effect on the minimum was linear. As predicted, and concurring with the significant relationship between ingesta and anatomical stratification (Fig. 2), % grass in species' diets decreased along an axis of increasing relative $\mathrm{SEF}_{\mathrm{dorsal\ rumen}}$, i.e. grass consumption was lowest in species with a less stratified papillation pattern ($R^2 = 0.93$, $p < 0.0001$; Fig. 3d). The effect was also significant for differences in maximum and minimum grass intake, but was again weaker for the former ($R^2 = 0.76$, $p < 0.0001$; Fig. 3e) than the latter ($R^2 = 0.93$, $p < 0.0001$; Fig. 3f). Phylogeny did not seem to influence these results (Table 1), suggesting a high degree of convergence in physiological and anatomical stratification with respect to diet.

The effect of a reduced grass intake along the axis of increasing relative $\mathrm{SEF}_{\mathrm{dorsal\ rumen}}$ is supported by analysis of a larger dataset (59 taxa; Clauss et al. 2009*c*). A similar negative exponential relationship was found for these 59 species ($R^2 = 0.64$, $p < 0.0001$; phylogenetically-controlled $R^2 = 0.54$, $p < 0.0001$; Fig. 4) as for the initial 11 taxa included in the study. Importantly, despite the difference in sample size, models for the two datasets yielded similar parameter estimates (Table 1) with overlapping 95% confidence intervals.

Interestingly, in our analysis of the larger dataset, there appeared to be two discernable "grades", which we identified as representing African and non-African species, respectively. When analyzed separately, the model for African taxa predicted a significantly stronger slope than for non-African taxa (95% CI: -0.038 to -0.073 and -0.023 to -0.032, respectively) but similar intercept. A stronger effect of stratification on diet amongst African taxa was also found for phylogenetically-controlled analyses (Table 1). No similar distinction between the strength of the stratification effect on diet could be made for Cervidae (slope -0.026, CI -0.010 to -0.041) compared with non-African Bovidae (slope -0.021, CI -0.007 to -0.036).

Testing effects of stratification: dietary variations in impala

Using model parameters derived for Figs 3d to 3f, and data for impala $\text{SEF}_{\text{dorsal rumen}}$ presented in Hofmann (1973), we calculated 'expected' diet values for this species. Although not included in our sample, impala are an interesting species for investigating the nature of ruminant diets because they are notorious mixed-feeders that switch and mix their diets across almost all levels of the browser-grazer continuum. This behaviour was exemplified in a study of regional and seasonal diet variations in the Kruger National Park, South Africa, based on carbon isotope analysis of faeces (Codron et al. 2006). Actual diet (the mean % grass intake for any one region or month) frequently exceeded the maximum predicted grass intake, but was never less than the predicted minimum (Table 2). Hofmann (1989) also proposed that seasonal diet switches, from browsing in the dry season to grazing in the wet season, are preceded by a change in rumen papillation patterns from homogeneously plentiful to a more stratified distribution. Adapting our calculations to incorporate seasonal differences in the relative $\text{SEF}_{\text{dorsal rumen}}$ (data for "browsing" and "grazing" impala in Hofmann 1973) did not impact the initial findings: impala never ate less grass than the predicted minimum, even in the wet season when the predicted level was as great as 33%. The seasonally-explicit approach also improved predictions for the maximum grass intake (Table 2).

Discussion

Although several previous studies have demonstrated differences in stratification across species with different diet niches (Hummel et al. 2005; Clauss et al. 2006*b*; Hummel et al. 2008*b*; Tschuor and Clauss 2008; Clauss et al. 2009*a*; Clauss et al. 2009*b*; Hummel et al. 2009; Lechner et al. 2010), no African bovid, with exception of the addax antelope *Addax nasomaculatus* (Blainville, 1816), was included in the investigations. African bovids were, so far, only included in data collections on anatomical proxies for rumen contents stratification and fluid throughput, such as the ruminal papillation pattern (Clauss et al. 2009*c*), and reticular and omasal anatomy (Clauss et al. 2006*a*; 2010*a*). Findings of this study suggest that physiological concepts on differences in rumen contents stratification and rumen fluid throughput developed mainly on ruminant species from the temperate zone can probably be transferred to many African species as well. The intraruminal papillation pattern, which already showed a good correlation with a physiological parameter describing contents stratification (the difference in fluid and particle passage, see Clauss et al. 2009*c*), also correlates with a simple physical measurement related to the same phenomenon (the difference in dorsal and ventral rumen fluid concentration), and can therefore be considered a good proxy for this crucial characteristic in ruminants. Both measures in the present study also produced similar results when related to botanical composition of species diets, highlighting the connection between anatomical differences between moose- and cattle-type ruminants and their respective diet niches.

It is necessary to consider some limitations to our data. The sample size is small, both in terms of number of individuals per species and the number of species for which we present data, and further observations are necessary to validate our results. Postmortem mixing of rumen contents is another potential concern, especially as animals used were not kept upright after being shot, but this is probably unavoidable for studies using dead rather than fistulated live animals (Clauss et al. 2009*b*). Nonetheless, it seems unlikely that these factors significantly altered arising patterns, qualitatively, and even quantitatively. For stratification of ingesta content, we found no quantitative differences between our data and published data for temperate species of similar feeding styles, despite the small sample size and thus greater standard deviations in the African dataset. Both datasets also produced similar effects when correlated with the relative SEF of the dorsal rumen. Although we only have data on ingesta stratification for 11 species, we also found very similar relationships between diet and relative SEF for both these data and a larger dataset of 59 taxa; therefore, it can be expected that data for ingesta content in other species will yield similar relationships with diet.

Our approach using diet as the dependent variable differs conceptually from many traditional approaches to ruminant diversification. In most studies, morphological and physiological traits are either compared between categorical feeding types (as in Fig. 1 of this study), or studied along a continuous axis of resource-use differentiation; for features related to diet, this axis is typically % grass or % browse in the natural diet as the independent variable (e.g. Pérez-Barbería et al. 2004; Mendoza and Palmqvist 2006; Codron et al. 2007*b*). Maybe often used simply for (unconscious) historical reasons, this approach focuses on functional morphophysiological differences of animals in different dietary niches. One major exception is Owen-Smith (1997), who discussed the facultative range of species’ diets with respect to Hofmann’s (1973) anatomical descriptions, and provided evidence to support anatomical and physiological constraints on the foraging preferences of browsers and grazers. Such an approach, although mainly a matter of choice rather than reflecting the nature of the data themselves, shifts the focus from the evolution of adaptations to the ecological consequences and implications of these adaptations.

The nonlinear relationships observed in some cases may have significance for interpreting ecological consequences. Many morphophysiological traits do not show a distinct linear relationship with dietary niche, i.e. % grass in the natural diet (Janis 1995; Clauss et al. 2006*a*; Codron et al. 2007*b*; Clauss et al. 2008*a*; Hofmann et al. 2008; Clauss et al. 2009*c*). Such effects could be expected if the two opposite ends of the perceived dichotomy – grass and browse – do not require alternatively exclusive adaptations, but a range of adaptations may correspond to the same dietary niche (see examples of hypsodont grazers and browsers in Mendoza et al. 2002). Alternatively, a nonlinear shape could also indicate threshold levels, above and below which utilization of the 'other' feeding niche becomes an option. Lechner et al. (2010) proposed that diet niche is not continuously related to rumen physiology, but above some threshold (where ruminants would be disadvantaged on anything but a strictly browse diet), niches can be expanded to mixed-feeding or even pure grazing. Their assertion is supported by the asymptotic-like (i.e. positive logarithmic) effect of stratification on mean % grass in species' natural diets observed in the current study. This pattern can be interpreted as indicating that % grass intake is held low (say < 20%) in species that lack stratification, but small increases in this capacity beyond a relatively low critical level rapidly or exponentially increase faculties for grazing. This hypothesis also explains why stratification appeared to place lesser constraints on the upper levels of grass consumption.

However, stratification seems to strongly constrain the minimum amount of grass a species will eat – at both inter- and intraspecific levels (see Fig. 3c, and Table 2), and thus diet niche does not necessarily expand indefinitely with stratification, but at some point becomes restricted to a maximum tolerable level of browse intake. A convenient explanation for this pattern is that animals that rely on browse material only must cope with a very high load of secondary plant compounds – which necessitate, apart from avoidance via selective feeding (Cooper and Owen-Smith 1985), salivary proteins that neutralize some of these compounds (Robbins et al. 1995; Fickel et al. 1998). These proteins might explain the observed greater rumen fluid viscosity observed in these ruminants (Robbins et al. 1995; Jones et al. 2001; Clauss et al. 2009*a*; Clauss et al. 2009*b*; Lechner et al. 2010), and the necessity for their production may be a reason for the larger salivary glands in 'moose-type' ruminants (Hofmann et al. 2008). However, this size difference may still not be large enough to allow 'moose-type' ruminants a greater saliva fluid production, which might represent a compromising effect due to the concomitant dilution of salivary proteins (Hofmann et al. 2008). In 'cattle-type' ruminants, rumen contents can be more stratified because production of high protein, viscous saliva is not necessary, and hence more non viscous saliva is produced.

Ruminants in Africa: special constraints due to C_4-grasses

Owen-Smith (1997) suggested that African ruminants are more constrained in their diet ranges because tropical C_4 grasses pose more of a challenge for digestion and nutrient extraction compared with C_3 grasses to which most ruminants in temperate and other climates are exposed. This phenomenon would account for the relative scarcity of true intermediate-feeders in Africa, whereas globally this is the most prominent feeding style (Hofmann 1989; Codron et al. 2008), and could also account for the lack of a true grazer guild amongst may temperate groups, notably the Cervidae (Geist 1999). Our analyses revealed that the effect of rumen stratification on diet is stronger in African ruminants compared with non-African species. Thus grazing African ruminants required a more pronounced increase in stratification (with presumably a greater intensity of the potentially advantageous effects of fluid throughput and stratification mentioned above), followed by a very sharp transition at some greater level. For non-African taxa, the slope of this trend approaches linearity, depicting an easier transition from a browse to a grass-based diet. These findings are in accord with the limited diet ranges of most African species, and suggest a physiological constraint to the ability of African species that do graze to switch to browse-rich diets. The observed difference could have been a historical coincidence because native cervids are absent from Africa, but there was no difference in the effect between Cervidae and non-African bovids. Phylogenetically-controlled analysis also indicate the effect was different for African versus non-African species (Table 1), further indicating an environmental (i.e. C_4 grass abundance) rather than taxonomic factor. A similar mechanism differentiating the evolution of craniodental traits in African and non-African taxa has also been suggested (Cerling et al. 2005; MacFadden 2005). At the very least, differences between C_4- and C_3-grass feeding warrant further investigation; we suggest, however, that all investigations of feeding style incorporating African and non-African taxa will need to explicitly differentiate between effects of these two very different grass sources.

Predictions for Ruminant Nutritional Ecology

Explanations for diet variations of ruminants, and their ecological consequences, are an important component of wildlife ecology and conservation biology (du Toit 2003; Owen-Smith 2008). Previously, reconciliation of the different approaches and outcomes of physiological investigations on gut constraints compared with ecological approaches to consumer behaviour have been approached mainly in terms of effects of gut capacity on intake (Owen-Smith 1994; Whelan and Brown 2005). We have advanced a physiological mechanism in ruminants that could define variations in specific diet compositions (see Searle and Shipley 2008 for further discussion on food selection). Diet variations in ruminants are mostly facultative, thus we do not suggest limitations imposed by digestive morphophysiology do not have to make feeding in alternate niches impossible. It is possible, for instance, to maintain a ‘moose-type’ ruminant on a purely grass-based diet or a ‘cattle-type’ ruminant on a purely browse-based diet – at least for a period of several weeks to months (Lechner et al. 2010), but there may be reductions in animal performance. As an example, differences in dental design (Kaiser et al. 2010) and mastication muscles (Clauss et al. 2008*a*) between browsing and grazing ruminants do not mean that the ingestion of the ‘other’ resource is a physical or physiological impossibility – it just translates into slight differences in chewing efficiency (Hummel et al. 2008*a*; Lechner et al. 2010). An important prediction we make is that whereas a ruminant might ingest a greater proportion of grass than indicated by its ‘predisposition to stratified rumen contents’ (because grass can physiologically be exploited even without a distinct stratification of rumen contents), it should not ingest a greater proportion of browse than indicated by this predisposition (because this predisposition is assumed to be the consequence of the production of defensive salivary proteins). We suggest that external factors of ecology and the environment are likely to become drivers of diet choice only when diet deviates above or below maximum and minimum levels of grass intake predicted by rumen stratification level; within this range nutrient acquisition might be such that diet choice is largely random, which could explain why herbivores are so often observed to feed, apparently, sub-optimally. Whether a reduction in grass intake below a predicted minimum leads to reduced fitness, e.g. body condition, growth, survivorship, or fertility, presents an interesting question for future study.

Acknowledgements

We thank Savvas Vrahmis, Frans Malie, James Brink, Nico Avenant, Jacqui Codron, Ethan Codron, Izak Thapo, Peter Mdala, Adam Thibeletsa, Thabiso Boleme, Bonny Nduma, Abel Dichakane and Werner Suter for facilitating fieldwork, assisting with rumen dissections, and sample handling. We thank Ian Newton and John Lanham for stable isotope analysis at the Stable Light Isotope Facility, Department of Archaeology, University of Cape Town, and Muzi Mkhohlwa for determinations of dry matter. J. Codron and an anonymous reviewer provided useful suggestions. Funding was provided by the National Research Foundation of South Africa, the University of KwaZulu-Natal, the National Museum, the Palaeontological Scientific Trust, the Swiss National Fund (IZ32Z0-125787) and the European Union (Marie-Curie PIIF-GA-2009-236670).

References

Bininda-Emonds, O.R.P., Cardillo, M., Jones, K.E., MacPhee, R.D.E., Beck, R.M.D., Grenyer, R., Price, S.A., Vos, R.A., Gittleman, J.L., and Purvis, A. 2007. The delayed rise of present-day mammals. Nature (Lond.). **446**: 507-512.

Cerling, T.E., and Harris, J.M. 1999. Carbon isotope fractionation between diet and bioapatite in ungulate mammals and implications for ecological and paleoecological studies. Oecologia, **120**: 347–363.

Cerling, T.E., Harris, J.M., and Leakey, M.G. 2005. Environmentally driven dietary adaptations in African mammals. *In* A history of atmospheric CO_2 and its effects on plants, animals and ecosystems. *Edited by* J.R. Ehleringer, T.E. Cerling, and M.D. Dearing. Springer, New York. pp. 258-272.

Clauss, M., Lechner-Doll, M., and Streich, W.J. 2003. Ruminant diversification as an adaptation to the physicomechanical characteristics of forage. A reevaluation of an old debate and a new hypothesis. Oikos, **102**: 253-262.

Clauss, M., Hofmann, R.R., Hummel, J., Adamczewski, J., Nygren, K., Pitra, C., Streich, W.J., and Reese, S. 2006a. The macroscopic anatomy of the omasum of free-ranging moose (*Alces alces*) and muskoxen (*Ovibos moschatus*) and a comparison of the omasal laminal surface area in 34 ruminant species. J. Zool. Lond. **270**: 346-358.

Clauss, M., Hummel, J., and Streich, W.J. 2006b. The dissociation of the fluid and particle phase in the forestomach as a physiological characteristic of large grazing ruminants: an evaluation of available, comparable ruminant passage data. Eur. J. Wildl. Res. **52**: 88-98.

Clauss, M., Hofmann, R.R., Streich, W.J., Fickel, J., and Hummel, J. 2008a. Higher masseter mass in grazing than in browsing ruminants. Oecologia, **157**: 377–385.

Clauss, M., Kaiser, T., and Hummel, J. 2008b. The morphophysiological adaptations of browsing and grazing mammals. *In* The ecology of browsing and grazing. *Edited by* I.J. Gordon, and H.H.T. Prins. Springer, Heidelberg. pp. 47-88.

Clauss, M., Fritz, J., Bayer, D., Hummel, J., Streich, W.J., Südekum, K.-H., and Hatt, J.M. 2009a. Physical characteristics of rumen contents in two small ruminants of different feeding type, the mouflon (*Ovis ammon musimon*) and the roe deer (*Capreolus capreolus*). Zoology, **112**: 195-205.

Clauss, M., Fritz, J., Bayer, D., Nygren, K., Hammer, S., Hatt, J.M., Südekum, K.-H., and Hummel, J. 2009b. Physical characteristics of rumen contents in four large ruminants of different feeding type, the addax (*Addax nasomaculatus*), bison (*Bison bison*), red deer (*Cervus elaphus*) and moose (*Alces alces*). Comp. Biochem. Physiol. A. **152**: 398-406.

Clauss, M., Hofmann, R.R., Fickel, J., Streich, W.J., and Hummel, J. 2009c. The intraruminal papillation gradient in wild ruminants of different feeding types: implications for rumen physiology. J. Morphol. **270**: 929–942.

Clauss, M., Hofmann, R.R., Streich, W.J., Fickel, J., and Hummel, J. 2010a. Convergence in the macroscopic anatomy of the reticulum in wild ruminant species of different feeding types and a new resulting hypothesis on reticular function. J. Zool. Lond. **281**: 26-38.

Clauss, M., Hume, I.D., and Hummel, J. 2010b. Evolutionary adaptations of ruminants and their potential relevance for modern production systems. Animal, **4**: 979-992.

Codron, D., Codron, J., Lee-Thorp, J.A., Sponheimer, M., de Ruiter, D., and Brink, J.S. 2006. Dietary variation in impala *Aepyceros melampus* recorded by carbon isotope composition of feces. Acta Zool. Sinica. **52**: 1015-1025.

Codron, D., Codron, J., Lee-Thorp, J.A., Sponheimer, M., de Ruiter, D., Sealy, J., Grant, R., and Fourie, N. 2007a. Diets of savanna ungulates from stable carbon isotope composition of faeces. J. Zool. (Lond.). **273**: 21-29.

Codron, D., Lee-Thorp, J.A., Sponheimer, M., Codron, J., de Ruiter, D., and Brink, J.S. 2007b. Significance of diet type and diet quality for ecological diversity of African ungulates. J. Anim. Ecol. **76**: 526-537.

Codron, D., Brink, J.S., Rossouw, L., and Clauss, M. 2008. The evolution of ecological specialization in southern African ungulates: competition or physical environmental turnover? Oikos, **117**: 344-353.

Cooper, S.M., and Owen-Smith, N. 1985. Condensed tannins deter feeding by browsing ruminants in a South African savanna. Oecologia, **67**: 142-146.

du Toit, J.T. 2003. Large herbivores and savanna heterogeneity. *In* The Kruger experience. *Edited by* J.T. du Toit, K.H. Rogers, and H.C. Biggs. Island Press, Washington DC. pp. 292-309.

Fickel, J., Göritz, F., Joest, B.A., Hildebrandt, T., Hofmann, R.R., and Breves, G. 1998. Analysis of parotid and mixed saliva in Roe deer (*Capreolus capreolus* L.). J. Comp. Physiol. B. **168**: 257-264.

Gagnon, M., and Chew, A.E. 2000. Dietary preferences in extant African Bovidae. J. Mammal. **81**: 490-511.

Geist, V. 1999. Deer of the world. Their evolution, behaviour, and ecology. Swan Hill Press, Shrewsbury.

Hofmann, R.R. 1973. The ruminant stomach. East African Literature Bureau, Nairobi.

Hofmann, R.R. 1989. Evolutionary steps of ecophysiological adaptation and diversification of ruminants: a comparative view of their digestive system. Oecologia, **78**: 443-457.

Hofmann, R.R., Streich, W.J., Fickel, J., Hummel, J., and Clauss, M. 2008. Convergent evolution in feeding types: salivary gland mass differences in wild ruminant species. J. Morphol. **269**: 240-257.

Hristov, A.N., Ahvenjärvi, S., McAllister, T.A., and Huhtanen, P. 2003. Composition and digestive tract retention time of ruminal particles with functional specific gravity greater or less than 1.02. J. Anim. Sci. **81**: 2639-2648.

Hummel, J., Clauss, M., Zimmermann, W., Johanson, K., Norgaard, C., and Pfeffer, E. 2005. Fluid and particle retention in captive okapi (*Okapia johnstoni*). Comp. Biochem. Physiol. A. **140**: 436-444.

Hummel, J., Fritz, J., Kienzle, E., Medici, E.P., Lang, S., Zimmermann, W., Streich, W.J., and Clauss, M. 2008a. Differences in fecal particle size between free-ranging and captive individuals of two browser species. Zoo Biol. **27**: 70-77.

Hummel, J., Steuer, P., Südekum, K.-H., Hammer, S., Hammer, C., Streich, W.J., and Clauss, M. 2008b. Fluid and particle retention in the digestive tract of the addax antelope (*Addax nasomaculatus*) – adaptations of a grazing desert ruminant. Comp. Biochem. Physiol. A. **149**: 142-149.

Hummel, J., Südekum, K.-H., Bayer, D., Ortmann, S., Hatt, J.M., Streich, W.J., and Clauss, M. 2009. Physical characteristics of reticuloruminal contents of cattle in relation to forage type and time after feeding. J. Anim. Physiol. Anim. Nutr. **93**: 209-220.

Janis, C.M. 1995. Correlations between craniodental morphology and feeding behavior in ungulates: reciprocal illumination between living and fossil taxa. *In* Functional morphology in vertebrate paleontology. *Edited by* J.J. Thomason. Cambridge University Press, Cambridge. pp. 76-98.

Jones, R.J., Meyer, J.H.F., Bechaz, F.M., Stolzt, M.A., Palmer, B., and van der Merwe, G. 2001. Comparison of rumen fluid from South African game species and from sheep to digest tanniniferous browse. Aust. J. Agric. Res. **52**: 453-460.

Kaiser, T.M., Fickel, J., Streich, W.J., Hummel, J., and Clauss, M. 2010. Enamel ridge alignment in upper molars of ruminants in relation to their natural diet. J. Zool. (Lond.). **281**: 12-25.

Lechner-Doll, M., Kaske, M., and Engelhardt, W.v. 1991. Factors affecting the mean retention time of particles in the forestomach of ruminants and camelids. *In* Physiological aspects of digestion and metabolism in ruminants. *Edited by* T. Tsuda, Y. Sasaki, and R. Kawashima. Academic Press, San Diego. pp. 455-482.

Lechner, I., Barboza, P., Collins, W., Fritz, J., Günther, D., Hattendorf, B., Hummel, J., Südekum, K.-H., and Clauss, M. 2010. Differential passage of fluids and different-sized particles in fistulated oxen (*Bos primigenius* f. *taurus*), muskoxen (*Ovibos moschatus*), reindeer (*Rangifer tarandus*) and moose (*Alces alces*): rumen particle size discrimination is independent from contents stratification. Comp. Biochem. Physiol. A. **155**: 211-222.

Lee-Thorp, J.A., and van der Merwe, N.J. 1987. Carbon isotope analysis of fossil bone apatite. S. Afr. J. Sci. **83**: 712-715.

MacFadden, B.J. 2005. Terrestrial mammalian herbivore response to declining levels of atmospheric CO_2 during the Cenozoic: evidence from North American fossil horses (family Equidae). *In* A history of atmospheric CO_2 and its effects on plants, animals and ecosystems. *Edited by* J.R. Ehleringer, T.E. Cerling, and M.D. Dearing. Springer, New York. pp. 273-292.

Maddison, W.P., and Maddison, D.R. 2008. Mesquite: A modular system for evolutionary analysis, V2.5. http://mesquiteproject.org.

Mendoza, M., Janis, C.M., and Palmqvist, P. 2002. Characterizing complex craniodental patterns related to feeding behaviour in ungulates: a multivariate approach. J. Zool. Lond. **258**: 223-246.

Mendoza, M., and Palmqvist, P. 2006. Characterizing adaptive morphological patterns related to diet in Bovidae (Mammalia: Artiodactyla). Acta Zool. Sinica. **52**: 988-1008.

Midford, P.E., Garland, T.J., and Maddison, W.P. 2003. PDAP Package.

Owen-Smith, N. 1982. Factors influencing the consumption of plant products by large herbivores. *In* Ecology of tropical savannas. *Edited by* B.J. Huntley, and B.H. Walker. Springer, Berlin, Heidelberg, New York. pp. 359-404.

Owen-Smith, N. 1994. Foraging responses of kudus to seasonal changes in food resources: Elasticity in constraints. Ecology, **75**: 1050-1062.

Owen-Smith, N. 1997. Distinctive features of the nutritional ecology of browsing versus grazing ruminants. Z Säugetierkd. **62**: 176-191.

Owen-Smith, N. 2008. The morphophysiological adaptations of browsing and grazing mammals. *In* The ecology of browsing and grazing. *Edited by* I.J. Gordon, and H.H.T. Prins. Springer, Heidelberg. pp. 149-178.

Pérez-Barbería, F.J., Elston, D.A., Gordon, I.J., and Illius, A.W. 2004. The evolution of phylogenetic differences in the efficiency of digestion in ruminants. Proc. R. Soc. Lond. B Biol. Sci. **271**: 1081-1090.

Quader, S., Isvaran, K., Hale, R.E., Miner, B.G., and Seavy, N.E. 2004. Nonlinear relationships and phylogenetically independent contrasts. J. Evol. Biol. **17**: 709-715.

Robbins, C.T., Spalinger, D.E., and Van Hoven, W. 1995. Adaptations of ruminants to browse and grass diets: are anatomical-based browser-grazer interpretations valid? Oecologia, **103**: 208-213.

Rutherford, M.C., and Westfall, R.H. 1994. Biomes of southern Africa: an objective classification. *In* Memoirs of the Botanical Survey of South Africa. *Edited by* National Botanical Institute, Pretoria. pp. 63-94.

Sakata, T., and Tamate, H. 1978. Rumen epithelial cell proliferation accelerated by rapid increase in intraruminal butyrate. J. Dairy Sci. **61**: 1109-1113.

Sakata, T., and Tamate, H. 1979. Rumen epithelial cell proliferation accelerated by propionate and acetate. J. Dairy Sci. **62**: 49-52.

Searle, K.R., and Shipley, L.A. 2008. The comparative feeding behaviour of large browsing and grazing herbivores. *In* The ecology of browsing and grazing. *Edited by* I.J. Gordon, and H.H.T. Prins. Springer, Heidelberg. pp. 117-148.

Sponheimer, M., Cerling, T.E., Robinson, T.F., Tegland, L., Roeder, B., Ayliffe, L., Dearing, M.D., and Ehleringer, J.R. 2006. Turnover of stable carbon isotopes in the muscle, liver and breath CO_2 of alpacas (*Lama pacos*) Rapid Commun. Mass Spectrom. **20**: 1-5.

Sponheimer, M., Lee-Thorp, J.A., de Ruiter, D.J., Smith, J.M., van der Merwe, N.J., Reed, K., Grant, C.C., Ayliffe, L.K., Robinson, T.F., Heidelberger, C., & Marcus, W. 2003. Diets of southern African Bovidae: Stable isotope evidence. J. Mammal. **84**: 471-479.

Statsoft_Inc. 2007. STATISTICA V8.0 (data analysis software system). www.statistica.com.

Tschuor, A., and Clauss, M. 2008. Investigations on the stratification of forestomach contents in ruminants: an ultrasonographic approach. Eur. J. Wildl. Res. **54**: 627-633.

Vogel, J.C. 1978. Isotopic assessment of the dietary habits of ungulates. S. Afr. J. Sci. **74**: 298-301.

Whelan, C.J., and Brown, J.S. 2005. Optimal foraging and gut constraints: reconciling two schools of thought. Oikos, **110**: 481-496.

Table 1. Statistics for regression models relating anatomical and physiological stratification proxies to % grass in the natural diet, including models based on raw data, and on phylogenetically independent contrasts. The lack of significant effects of body mass on these data are also shown.

		Analysis of raw data				**Analysis of independent contrasts**		
Effect	**Response variable**	**R^2 (best-fit)**	***p***	**Intercept**	**Slope**	**R^2**	***p***	**Slope**
11 taxa with DM data available								
DM difference	% grass (mean)	0.93 (log)	<0.0001	11.558	42.310	0.91	<0.0001	39.160
	% grass (max)	0.78 (log)	<0.0001	32.136	36.765	0.71	<0.01	37.554
	% grass (min)	0.91 (lin)	<0.0001	3.284*	13.645	0.82	<0.001	37.689
SEF $_{\text{dorsal rumen}}$ (% of SEF$_{\text{atrium}}$)	% grass (mean)	0.93 (exp)	<0.0001	122.684	-0.055	0.89	<0.0001	-40.019
	% grass (max)	0.76 (exp)	<0.0001	113.648	-0.027	0.82	<0.001	-37.689
	% grass (min)	0.93 (exp)	<0.0001	138.525	-0.104	0.76	<0.001	-39.852
Body mass	DM difference	0.08 (lin)	0.31	1.658*	0.008*	0.13	0.28	-0.286
	SEF $_{\text{dorsal rumen}}$ (% of SEF$_{\text{atrium}}$)	0.04 (lin)	0.06	29.572*	-0.046*	0.16	0.23	0.324
	% grass (mean)	0.02 (lin)	0.05	48.536*	0.050*	0.06	0.46	8.456
	%grass (max)	0.00 (lin)	<0.05	70.076	0.005*	0.01	0.73	4.289
	%grass (min)	0.06 (lin)	0.24	28.031*	0.090*	0.12	0.30	11.745
59 taxa from (Clauss et al. 2009c)								
SEF $_{\text{dorsal rumen}}$ (% of SEF$_{\text{atrium}}$)	% grass (mean)	0.64 (exp)	<0.0001	101.821	-0.034	0.54	<0.0001	-29.550
Body mass	SEF $_{\text{dorsal rumen}}$ (% of SEF$_{\text{atrium}}$)	0.01 (lin)	0.38	30.782	-0.016*	0.00	0.60	-0.051
	% grass (mean)	0.03 (lin)	0.16	41.888	0.038*	0.00	0.96	0.205
29 African Bovidae and Giraffe (Giraffa camelopardalis)*:*								
SEF $_{\text{dorsal rumen}}$ (% of SEF$_{\text{atrium}}$)	% grass (mean)	0.82 (exp)	<0.0001	114.072	-0.055	0.73	<0.0001	-35.744
30 non-African taxa:								
SEF $_{\text{dorsal rumen}}$ (% of SEF$_{\text{atrium}}$)	% grass (mean)	0.57 (exp)	<0.0001	93.197	-0.023	0.50	<0.0001	-25.628

DM difference = arithmetic difference in dry matter concentration between dorsal and ventral rumen content; SEF = surface enlargement factor; % grass = % grass in the natural diet (models for mean % grass, maximum % grass, and minimum % grass in the diet); BM = body mass; exp = exponential regression model, log = logarithmic regression model, lin = linear regression model (selected on best-fit, i.e. lowest residual variance); Analysis of phylogenetically independent contrasts was by linear least squares regression through the origin, using ln-transformed data for DM difference, relative SEF, and Body mass.

* Indicates parameter estimate not significantly different from zero.

Table 2. Comparison between measured % grass in the diet of impala *Aepyceros melampus* (Lichtenstein, 1812), estimated from δ^{13}C of faeces from Kruger National Park, South Africa (Codron et al. 2006), with diet ranges predicted based on ruminal papillation patterns.

Season	SEF dorsal rumen (% of atrium)	Empirical data			Predicted			% occurrences:	
		Mean	Max	Min	Mean	Max	Min	> Max	< Min
Overall	25	60	88	16	31	58	10	63	0
Dry season	33	54	82	5	20	46	4	33	0
Wet season	14	66	88	33	57	78	32	10	0

Predicted diets modeled using derived relationships between % grass in the natural diet with the relative SEF of the dorsal rumen (Fig. 3; Table 1). Data for seasonal differences in SEF are based on Hofmann (1973) for “browsing” and “grazing” seasons, respectively.

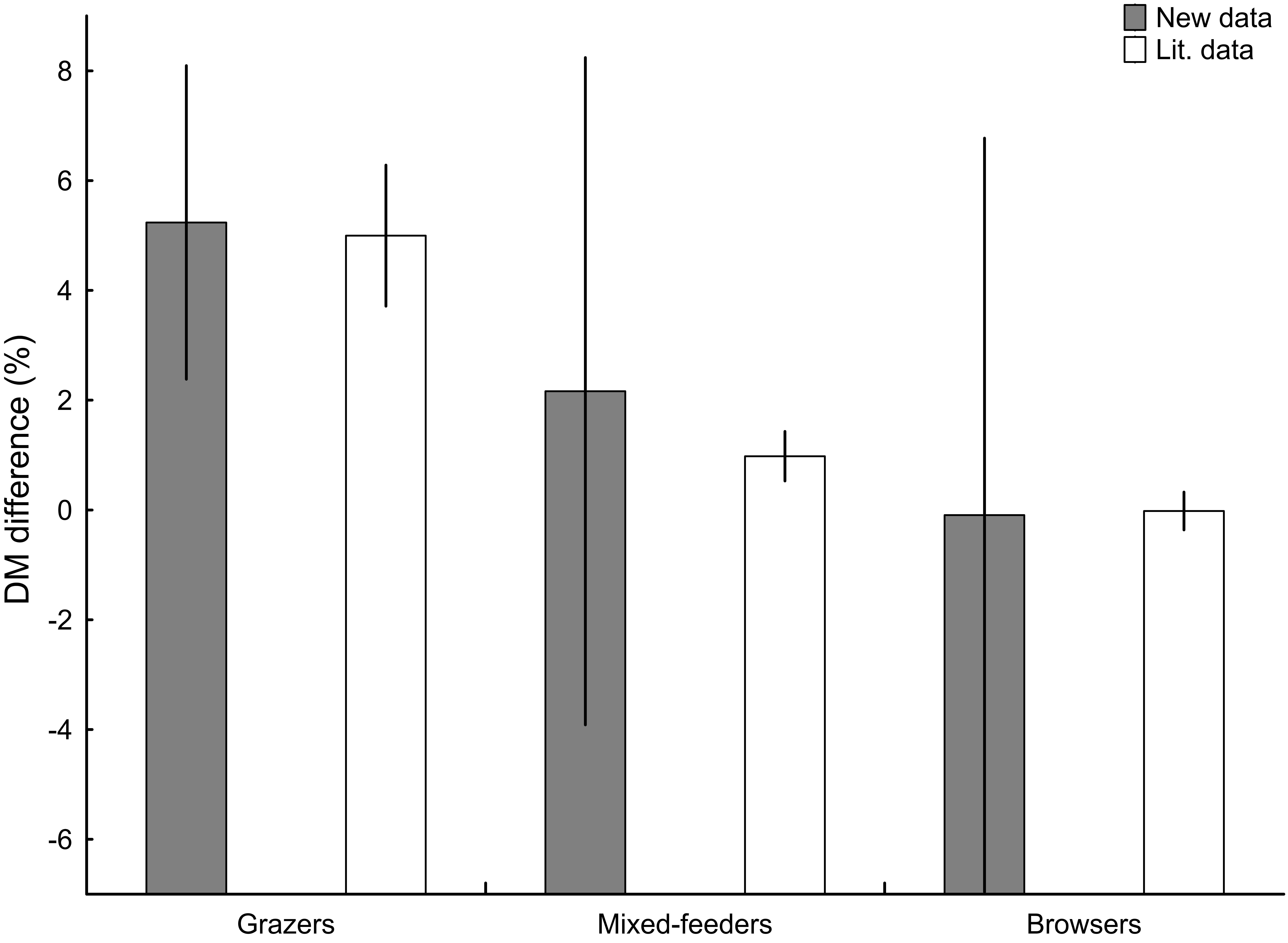
Figure Legends

Figure 1. Mean pairwise differences (with 95% confidence intervals) between dorsal and ventral rumen DM (% dry matter) content across 11 ruminant species with different feeding styles. Grazers are species with mean % grass consumption >80%, browsers consume <10% grass on average; New data = data for African ruminants generated in this study; Lit. data = previously published data (see supplementary material for details).

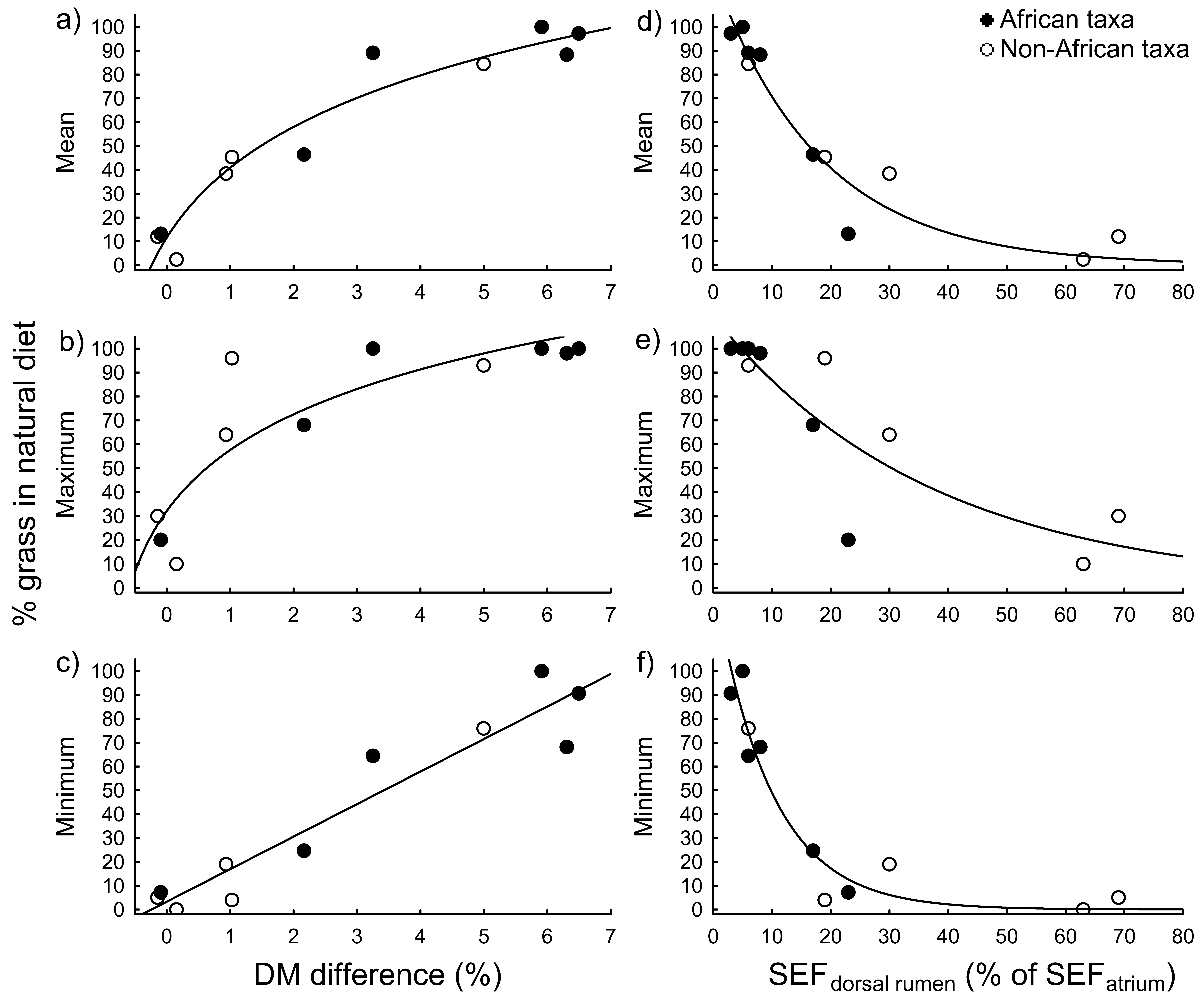
Figure 2. Relationship between physiological (difference between DM concentration between dorsal and ventral rumen) and the intraruminal papillation pattern. Note that a decrease in relative SEF reflects a larger difference in papillation of the dorsal rumen relative to the atrium, and hence an increased ‘anatomical stratification’. The curve represents least-squares exponential regression ($y = 48.706e^{-0.527x}$; $R^2 = 0.71$, $p < 0.001$). DM data for African taxa were generated in this study; data for non-African taxa are from Clauss et al. (2009a; 2009b). Rumen papillation data are from Clauss et al. (2009c).

Figure 3. Relationships between rumen contents stratification (a-c) and rumen papillation pattern on the mean (a, d), maximum (b, e), and minimum (c, f) % grass in the natural diet of 11 ruminant species. Curves represent least-squares linear or exponential regression models (see Table 1 for details).

Figure 4. Relationship beteen rumen papillation pattern and mean % grass in the natural diet of 59 ruminant species (data from Clauss et al. 2009c). Note the differences between African compared with non-African species. Curves represent least-squares exponential regression models (see Table 1 for details).


New data
Lit. data
8
6
4
2
0
-2
-4
-6
DM difference (%)
Grazers
Mixed-feeders
Browsers

80
70
60
50
40
30
20
10
0
SEF_{dorsal rumen} (% of SEF_{atrium})
0
1
2
3
4
5
6
7
DM difference (%)
● African taxa
○ Non-African taxa


a)
b)
c)
d)
e)
f)
% grass in natural diet
Mean
Maximum
Minimum
DM difference (%)
SEF dorsal rumen (% of SEF atrium)
African taxa
Non-African taxa
0
10
20
30
40
50
60
70
80
90
100
0
1
2
3
4
5
6
7
0
10
20
30
40
50
60
70
80


African taxa
Non-African taxa
mean % grass in natural diet
0
10
20
30
40
50
60
70
80
90
100
$SEF_{dorsal\ rumen}$ (% of SEF_{atrium})
0
10
20
30
40
50
60
70
80
90
100

Supplementary Table S1. Mean percent dry matter, DM, (± 1 standard error) of dorsal and ventral rumen content, surface enlargement factor (SEF) for the dorsal rumen, mean body mass of females, and δ^{13}C of the rumen epithelium (and/or % grass in the natural diet), for 11 ruminant species used in this study.

		DM$_{\text{rumen content}}$ (%)				**SEF$_{\text{dorsal rumen}}$(% of SEF$_{\text{atrium}}$)**	**BM (kg)**	**δ^{13}C$_{\text{rumen tissue}}$**		**% Grass in natural diet**		
Species	**Common name**	***n***	**Dorsal**	**Ventral**	**Difference**			***n***	**‰ (VPDB)**	**Mean**	**Max**	**Min**
Alcelaphus buselaphus	Red hartebeest	2	26.7	20.8	5.9	5[C]	174[C]	2	-10.9	100*	100	100
Antidorcas marsupialis	Springbok	10	21.5 ± 1.3	19.3 ± 1.9	2.2 ± 2.7	17[C]	41[C]	9	-18.8 ± 0.8	46*	68	25
Connochaetes gnou	Black wildebeest	5	29.0 ± 1.6	22.5 ± 3.3	6.5 ± 3.8	3[C]	170[D]	5	-11.4 ± 0.4	97*	100	91
Damaliscus pygargus phillipsi	Blesbok	6	21.5 ± 1.1	18.2 ± 1.1	3.3 ± 1.9	6[C]	61[D]	6	-12.6 ± 0.8	89*	100	64
Oryx gazella	Gemsbok	4	26.8 ± 1.9	20.5 ± 3.1	6.3 ± 2.3	8[C]	182[C]	4	-12.7 ± 1.0	88*	98	68
Tragelaphus strepsiceros	Greater kudu	3	23.3 ± 2.0	23.4 ± 0.9	-0.1 ± 1.6	23[C]	214[C]	3	-23.6 ± 0.5	13*	20	7
Alces alces	Moose	17	15.2 ± 0.8[A]	15.1 ± 0.8[A]	0.2 ± 0.4	63[C]	258[C]			2[1-12]	10	0
Bison bison	Bison	10	13.2 ± 0.3[A]	8.2 ± 0.6[A]	5.0 ± 0.6	6[C]	335[C]			85[13,14]	93	76
Capreolus capreolus	Roe deer	23	12.9 ± 0.3[B]	13.1 ± 0.3[B]	-0.1 ± 0.1	69[C]	25[C]			12[1,4,15-19]	30	5
Cervus elaphus	Red deer	17	15.0 ± 0.2[A]	13.9 ± 0.3[A]	1.0 ± 0.2	19[C]	170[C]			45[15,20-47]	96	4
Ovis ammon musimon	Mouflon	19	16.7 ± 0.4[B]	15.8 ± 0.4[B]	0.9 ± 0.4	30[C]	40[C]			38[48-54]	64	19

n = number of individuals; * = estimated from stable C isotope data, using a linear two-source mixing model; other data sources sourced from the literature (note that SEF data representing *Connochaetes gnou* and *Damaliscus pygargus phillipsi* are for *C. taurinus* and *D. lunatus,* respectively):[A]Clauss et al. (2009a);[B]Clauss et al. (2009b);[C]Clauss et al. (2009c);[D]Skinner and Smithers (1990);[1]Cederlund et al. (1980);[2]Cushwa and Coady (1976);[3]Dorn (1983);[4]Dzięciołowski et al. (1975);[5]Harry (1957);[6]Hosley (1949);[7]Knowlton (1960);[8]McMillan (1953);[9]Morow (1976);[10]Peterson (1955);[11]Schwartz (1992);[12]Stevens et al. (2006);[13]Breymeyer and Dyne (1980);[14]Larter and Gates (1991);[15]Gębczyńska (1980);[16]Henry (1978);[17]Hosey (1981);[18]Jackson (1980);[19]Schröder and Schröder (1984);[20]Albon et al. (1992);[21]Baker and Hobbs (1983);[22]Chen et al. (1998);[23]Collins and Urness (1983);[24]Constan (1972);[25]Dzięciołowski (1967);[26] Dzięciołowski (1970);[27]Edge et al. (1983);[28]Hansen and Clark (1977);[29]Harper et al. (1967);[30]Hobbs et al. (1981);[31]Homolka (1990);[32]Jensen (1968);[33]Kirchhoff and Larsen (1998);[34]Korfhage et al. (1980);[35]Kuen and Bubenik (1980);[36]Kufeld (1973);[37]Latham et al. (1999);[38]Leslie et al. (1984);[39]McCorquodale (1993);[40]Morris and Schwartz (1957);[41]Olsen and Hansen (1976);[42]Pickfford and Reid (1943);[43]Rowland et al. (1983);[44]Staines and Crisp (1978);[45]Staines et al. (1982);[46]Vaag (1980);[47]Wydeven and Dahlgren (1983);[48]Briedermann (1986);[49]Faliu et al. (1990);[50]Garcia-Gonzalez and Cuartas (1989);[51]Hadjisterkotis (1996);[52]Heroldova (1988);[53]Homolka (1991);[54]Thiele et al. (1989)

References

Albon, S.D., Clutton-Brock, T.H., and Langvatn, R. 1992. Cohort variation in reproduction and survival: Implications for population demography. *In* The biology of deer. *Edited by* R.D. Brown. Springer-Verlag, Berling. pp. 15-21.

Baker, D.L., and Hobbs, N.T. 1983. Composition and quality of elk summer diets in Colorado. J. Wildl. Manag. **46**: 694-703.

Breymeyer, A.I., and Dyne, G.M.V. 1980. Grasslands, systems analysis and man. Cambridge University Press,

Briedermann, L. 1986. Untersuchungen zur Nahrungswahl bei Muffelwild im ersten Lebensjahr. Beiträge zur Jagd- und Wildforschung. **14**: 155-162.

Cederlund, G., Ljungquist, H., Markgren, G., and Stålfelt, F. 1980. Foods of moose and Roe deer at Grimsø in Central Sweden - results of rumen content analyses. Swedish Wildl. Res. **11**: 169-247.

Chen, H., Jianzhang, M.A., Li, F., Sun, Z., Wang, H., Luo, L., and Li, F. 1998. Seasonal composition and quality of red deer *Cervus elaphus* diets in northeastern China. Acta Theriol. **43**: 77-94.

Clauss, M., Fritz, J., Bayer, D., Hummel, J., Streich, W.J., Südekum, K.-H., and Hatt, J.M. 2009a. Physical characteristics of rumen contents in two small ruminants of different feeding type, the mouflon (*Ovis ammon musimon*) and the roe deer (*Capreolus capreolus*). Zoology, **112**: 195-205.

Clauss, M., Fritz, J., Bayer, D., Nygren, K., Hammer, S., Hatt, J.M., Südekum, K.-H., and Hummel, J. 2009b. Physical characteristics of rumen contents in four large ruminants of different feeding type, the addax (*Addax nasomaculatus*), bison (*Bison bison*), red deer (*Cervus elaphus*) and moose (*Alces alces*). Comp. Biochem. Physiol. A. **152**: 398-406.

Clauss, M., Hofmann, R.R., Fickel, J., Streich, W.J., and Hummel, J. 2009c. The intraruminal papillation gradient in wild ruminants of different feeding types: implications for rumen physiology. J. Morphol. **270**: 929–942.

Collins, W.B., and Urness, P.J. 1983. Feeding behaviour and habitat selection of mule deer and elk on northern Utah summer range. J. Wildl. Manag. **47**: 646-663.

Constan, K.J. 1972. Winter foods and range use of three species of ungulates. J. Wildl. Manag. **36**: 1068-1076.

Cushwa, C.T., and Coady, J. 1976. Food habits of moose (*Alces alces*) in Alaska: a preliminary study using rumen contents analysis. Can. Field-Nat. **90**: 11-16.

Dorn, R.D. 1983. Moose and cattle food habits in southwest Montana. J. Wildl. Manag. **34**: 559-564.

Dzięciołowski, R. 1967. Food of the red deer in an annual cycle. Acta Theriol. **12**: 503-520.

Dzięciołowski, R. 1970. Foods of the red deer as determined by rumen content analyses. Acta Theriol. **15**: 89-110.

Dzięciołowski, R., Kossak, S., Borowski, S., and Morow, K. 1975. Diets of big herbivorous mammals. Pol. Ecol. Stud. **1**: 33-50.

Edge, W.D., Marcum, C.L., and Olson-Edge, S.L. 1983. Summer forage and feeding site selection by elk. J. Wildl. Manag. **52**: 573-577.

Faliu, L., Cugnasse, J.M., Auvray, F., Orliac, D., and Rech, J. 1990. Le régime alimentaire du mouflon de Corse dans le massif du Caroux-Espinouse d'après l'analyse du contenu de 125 panses. Rev. Med. Vet. **141**: 545-556.

Garcia-Gonzalez, R., and Cuartas, P. 1989. A comparison of the diets of the wild goat (*Capra pyrenaica*), domestic goat (*Capra hircus*), mouflon (*Ovis musimon*) and domestic sheep (*Ovis aries*) in the Cazorla Mountain Range. Acta Biol. Mont. **9**: 123-132.

Gębczyńska, Z. 1980. Food of the roe deer and red deer in the Białowieża primeval forest. Acta Theriol. **25**: 487-500.

Hadjisterkotis, E. 1996. Food habits of the Cyprus mouflon (*Ovis gmelini ophion*). Z. Jagdwissenschaft. **42**: 256-263.

Hansen, R.M., and Clark, R.C. 1977. Foods of elk and other ungulates at low elevations in northwestern Colorado. J. Wildl. Manag. **41**: 76-80.

Harper, J.A., Harn, J.H., Bentley, W.W., and Yocom, C.F. 1967. The status and ecology of the Roosevelt elk in California. Wildl. Monogr. **16**: 3-49.

Harry, G.B. 1957. Winter food habits of moose in Jackson Hole, Wyoming. J. Wildl. Manag. **21**: 53-57.

Henry, B.A.M. 1978. Diet of roe deer in an English conifer forest. J. Wildl. Manag. **42**: 937-940.

Heroldova, M. 1988. The diet of Mouflon (*Ovis musimon*) outside the growing period 1983 - 1984. Folia Zool. **37**: 309-318.

Hobbs, N.T., Baker, D.L., Ellis, J.E., and Swift, D.M. 1981. Composition and quality of elk winter diets in Colorado. J. Wildl. Manag. **45**: 156-171.

Homolka, M. 1990. Food of *Cervus elaphus* in the course of the year in the mixed forest habitat of the Drahanská vrchovina highlands. Folia Zool. **39**: 1-13.

Homolka, M. 1991. The diet of moufflon (*Ovis musimon*) in the mixed forest habitat of the Drahanska Vrchovina highland. Folia Zool. **40**: 193-201.

Hosey, G.R. 1981. Annual foods of the roe deer (*Capreolus capreolus*) in the south of England. J. Zool. (Lond.). **194**: 276-278.

Hosley, N.W. 1949. The moose and its ecology. US Fish & Wildlife Service, Wildlife Leaflet. **312**: 1-51.

Jackson, J.E. 1980. The annual diet of the roe deer (*Capreolus capreolus*) in the New Forest, Hampshire, as determined by rumen content analysis. J. Zool. (Lond.). **192**: 71-83.

Jensen, P.V. 1968. Food selection of the Danish red deer (*Cervus elaphus*) as determined by examination of the rumen content. Dan. Rev. Game Biol. **5**: 1-42.

Kirchhoff, M.D., and Larsen, D.N. 1998. Dietary overlap between native sitka black-tailed deer and introduced elk in southeast Alaska. J. Wildl. Manag. **62**: 236-242.

Knowlton, F.F. 1960. Food habits, movements and populations of moose in the Gravelly Mountains, Montana. J. Wildl. Manag. **24**: 162-170.

Korfhage, R.C., Nelson, J.R., and Skovlin, J.M. 1980. Summer diets of Rocky Mountain elk in northeastern Oregon. J. Wildl. Manag. **44**: 746-750.

Kuen, H., and Bubenik, A.B. 1980. Botanische Pansenanalysen bei Rotwild (*Cervus elaphus hippelaphus*), Rehwild (*Capreolus capreolus*) und Gamswild (*Rupicapra rupicapra*). Ergebn. d. Forschungsproj. Achenkirch. **A67**:

Kufeld, R.C. 1973. Foods eaten by the Rocky Mountain elk. J. Range Manag. **26**: 106-113.

Larter, N.C., and Gates, C.C. 1991. Diet and habitat selection of wood bison in relation to seasonal changes in forage quantity and quality. Can. J. Zool. **69**: 2677-2685.

Latham, J., Staines, B., and Gorman, M.L. 1999. Comparative feeding ecology of red deer (*Cervus elaphus*) and roe deer (*Capreolus capreolus*) in Scottish plantation forests. J. Zool. (Lond.). **247**: 409-418.

Leslie, D.M.J., Starkey, E.E., and Vavra, M. 1984. Elk and deer diets in old-growth forests in western Washington. J. Wildl. Manag. **48**: 762-775.

McCorquodale, S.M. 1993. Winter foraging behavior of elk in the shrub-steppe of Washington. J. Wildl. Manag. **57**: 881-890.

McMillan, J.F. 1953. Some feeding habits of moose in Yellowstone Park. Ecology, **34**: 102-110.

Morow, K. 1976. Food habits of moose from Augustow Forest. Acta Theriol. **21**: 101-116.

Morris, M.S., and Schwartz, J.E. 1957. Mule deer and elk food habits on the National Bison Range. J. Wildl. Manag. **21**: 189-193.

Olsen, F.W., and Hansen, R.M. 1976. Food relations of wild free-roaming horses to livestock and big game, red desert, Wyoming. J. Range Manag. **30**: 17-20.

Peterson, R.L. 1955. North American moose. University of Toronto Press, Toronto.

Pickford, G.D., and Reid, E.H. 1943. Competition of elk and domestic livestock for summer range forage. J. Wildl. Manag. **7**: 328-332.

Rowland, M.M., Alldredge, A.W., Ellis, J.E., Weber, B.J., and White, G.C. 1983. Comparative winter diets of elk in New Mexico. J. Wildl. Manag. **47**: 924-932.

Schröder, J., and Schröder, W. 1984. Niche breadth and overlap in red deer (*Cervus elaphus*), roe deer (*Capreolus capreolus*) and chamois (*Rupicapra rupicapra*). Acta Zool. Fenn. **172**: 85-86.

Schwartz, C.C. 1992. Physiological and nutritional adaptations of moose to Northern environments. Alces Suppl. **1**: 139-155.

Skinner, J.D., and Smithers, R.H.N. 1990. The mammals of the southern African subregion. University of Pretoria, Pretoria.

Staines, B.W., and Crisp, J.M. 1978. Observations on food quality in Scottish red deer (*Cervus elaphus*) as determined by chemical analysis of the rumen contents. J. Zool. (Lond.). **185**: 253-259.

Staines, B.W., Crisp, J.M., and Parish, T. 1982. Differences in the quality of food eaten by red deer (*Cervus elaphus*) stags and hinds in winter. J. Appl. Ecol. **19**: 65-77.

Stevens, R., Lister, A., and Hedges, R. 2006. Predicting diet, trophic level and palaeoecology from bone stable isotope analysis: a comparative study of five red deer populations. Oecologia, **149**: 12-21.

Thiele, E., Peukert, R., and Prien, S. 1989. Die Nahrungswahl des Muffelwildes im Einstandgebiet Ostharz in Abhängigkeit von der Jahreszeit. Beiträge zur Jagd- und Wildforschung. **16**: 71-77.

Vaag, A.B. 1980. Comparative nutritional investigations in red deer (*Cervus elaphus*) and sheep (Selbjørnsau) (in Norwegian). M.Sc. thesis, Agricultural University of Norway, Ås.

Wydeven, A.P., and Dahlgren, R.B. 1983. Food Habits of Elk in the Northern Great Plains. J. Wildl. Manag. **47**: 916-923.