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# Significance of diet type and diet quality for ecological diversity of African ungulates

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## Summary

1. We test two nutritional hypotheses for the ecological diversity of ungulates, the browser/grazer (diet type) and diet quality models, among free-ranging herbivores in a South African savanna, the Kruger National Park. Tests are based on assessment of relationships between diet type and diet quality with body mass and hypsodonty, two morphological features that have been associated with both elements.
2. We use stable carbon isotope ratios of faeces to reconstruct diet in terms of proportions of C<sub>3</sub> plants (browse) and C<sub>4</sub> plants (grass) consumed by different species in different seasons. These data are combined with proxies for diet quality (per cent nitrogen, neutral detergent fibre, acid detergent fibre, and acid detergent lignin) from faeces to track changes in diet quality.
3. Two statistical approaches are used in model selection, i.e. tests of significant correlations based on linear regression analyses, and an information-theory approach (Akaike's Information Criterion) providing insight into strength of evidence for models.
4. Results of both methods show that, contrary to many predictions, body mass and diet type are not related, but these data confirm predictions that diet quality decreases with increasing body size, especially during the dry season. Hypsodonty, as expected, varies with diet type, increasing with increased grass intake.
5. These findings support both a diet type and diet quality model, implying some degree of exclusivity. We propose that congruence between models may be achieved through addition of diet quality proxies not included here, because hypsodonty is more likely a reflection of the abrasive properties of consumed foods, i.e. related to food quality, rather than food type. This implies that adaptation to diets of varying quality, through changes in body size and dental features, has been the primary mechanism for diversification in ungulates.
6. Our interpretation contrasts with several recent studies advocating diet type as the primary factor, exemplifying that further reconciliation between the two models is needed. We discuss the implications of this study for future approaches to achieve a more cohesive understanding of the evolutionary outcomes of herbivore nutrition.

*Key-words:* body mass, carbon isotopes, fibre, hypsodonty, per cent nitrogen.

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## Introduction

The exceptional species diversity of ungulates has been described from a browser/grazer model of differentiation, based on differences in the types of food these herbivores

eat, i.e. a diet type model. Features including digestive anatomy and morphophysiology, body size, and oral and dental morphology have been functionally related to browsing and grazing (Bell 1970; Hofmann & Stewart 1972; Jarman 1974; Demment & Van Soest 1985; Janis 1988; Owen-Smith 1988; Hofmann 1989; Gagnon & Chew 2000; Perez-Barberia & Gordon 2001). Despite its widespread acceptance, however, the validity of browser/grazer interpretations is still heavily debated (reviewed in Ditchkoff 2000). One confounding factor is diet quality, which is predicted to influence digestive physiology, body size and oral morphology (Bell 1970; Jarman 1974; Demment & Van Soest 1985; Janis 1988; Owen-Smith 1988; Illius & Gordon 1992; Gordon & Illius 1994, 1996; Robbins, Spalinger & van Hoven 1995; Perez-Barberia & Gordon 2001). Gordon & Illius (1994, 1996) even argued that diet quality is the primary determinant of niche diversity, i.e. a diet quality model.

Testing dietary hypotheses has been constrained by the conventional approach of categorizing species into discrete feeding guilds (browser, grazer or mixed-feeder), which requires arbitrary definitions of boundaries, and often leads to circularity (see Clauss, Lechner-Doll & Streich 2003; Perez-Barberia *et al.* 2004). Collating published data from field studies carried out over disparate spatial and temporal scales also gives rise to inconsistent accounts of species' natural diets (see Owen-Smith 1988; Cerling, Harris & Passey 2003; Sponheimer *et al.* 2003a). Stable carbon isotope ecology provides a uniform means to express diet as a continuous variable. In African savannas,  $^{13}\text{C}/^{12}\text{C}$  ratios of herbivore tissues record proportions of  $\text{C}_3$  (trees, shrubs and forbs) to  $\text{C}_4$  (grass) biomass consumed (Vogel 1978; Lee-Thorp & van der Merwe 1987; Cerling & Harris 1999), making them ideally suited to testing hypotheses related to browsing and grazing (Cerling *et al.* 2003; Sponheimer *et al.* 2003a). The carbon isotope composition of herbivore faeces also reflects that of the diet, and appears not to be influenced by potential differences in digestibility of browse and grass (Tieszen *et al.* 1979; Sponheimer *et al.* 2003b; D. Codron *et al.* 2005). Faeces are especially useful because they have a relatively short turnover time (several days) and hence record subtle variations in diet, e.g. through the seasonal cycle.

Data for variations in diet quality and digestive efficiency of free-ranging animals are also scarce. Information about digestive physiology is available mostly from controlled-feeding experiments, but while these yield valuable data, insights are limited because the animals are not exposed to the same diets and array of environmental stimuli they experience in free-ranging conditions. Per cent nitrogen of faeces is a well-established measure of diet quality, reflecting (at least roughly) crude protein content of the diet (Erasmus, Penzhorn & Fairall 1978; Holecheck, Vavre & Pieper 1982; Leslie & Starkey 1985). Fibre content (neutral detergent fibre NDF, acid detergent fibre ADF, and acid detergent lignin ADL) of faeces has also been used to track changes in diet quality (e.g. Erasmus *et al.*

1978; Dörgeleh, van Hoven & Rethman 1998), although data may be influenced by differential digestive efficiencies.

Here, we test whether morphological adaptations in African savanna ungulates reflect variations in diet type or quality, using stable carbon isotope evidence for diet and faecal proxies for diet quality. We focus on body mass and hypsodonty (molar crown height), features commonly associated with proportions of browse and grass intake but also predicted to vary with diet quality (e.g. Bell 1970; Jarman 1974; Janis 1988). Two previous studies have used carbon isotope data from body tissues of East and southern African Bovidae, respectively, to test predictions for relationships between proportions of grass consumed with body mass and hypsodonty (Cerling *et al.* 2003; Sponheimer *et al.* 2003a). Notably, these studies differed with respect to findings for body mass, in that significant correlations between diet and body size were only recorded for East African, but not southern African, bovids. Our results are for faeces from South Africa's Kruger National Park, controlling for the effects of dry and wet season changes to assess relationships between diet, diet quality and morphology.

## Methods

The Kruger National Park is a large (c.2 000 000 ha) semiarid savanna, situated in the north-east of South Africa between the latitudes  $22^{\circ}20'S$  and  $25^{\circ}32'S$ , and the longitudes  $30^{\circ}53'E$  and  $32^{\circ}02'E$ . Mean annual rainfall varies between 500 and 700 mm in the south to between 300 and 500 mm in the north, but is highly seasonal, falling mainly during the summer months between October and March, while April to November are dry (Venter, Scholes & Eckhardt 2003). The area is divided longitudinally into granitic substrates forming nutrient poor soils in the west, and nutrient rich basaltic soils in the east (Venter *et al.* 2003). The northern regions (to the north of the centrally located Olifants River) are dominated by mopane *Colophospermum mopane* 'shrubveld' and woodland, while fine-leaved *Acacia* and *Combretum* savannas abound in the south. Fresh, i.e. damp or wet, faeces of 19 ungulate species (seven browsers, two mixed-feeders, and 10 grazers) were collected from June 2002 to May 2005, biannually during the first 2 years, and monthly from February 2004 to May 2005. Where possible, we selected specimens from a single landscape, the northern basalt grasslands, but taxa that are rare/absent in this landscape had to be selected from elsewhere in Kruger Park (see electronic appendix, Table S1).

Faeces were oven-dried at  $60^{\circ}\text{C}$  for 24 h, and mill-ground into a homogeneous powder through a 1-mm sieve. Powdered samples were individually combusted in an automated Elemental Analyser (Carlo Erba, Milan), and the resultant  $\text{CO}_2$  gas introduced to a MAT 252 or DELTA XP Mass Spectrometer (Finnigan, Bremen) via a continuous flow-through inlet system

(Conflo).  $^{13}\text{C}/^{12}\text{C}$  ratios are expressed in the delta ( $\delta$ ) notation in parts per mil (‰) relative to the Vienna PeeDee Belemnite (VPDB) standard. Standard deviations of repeated measurements of laboratory plant, protein, and chocolate standards were less than 0.1‰. Simultaneous combustion of  $\text{N}_2$  gas yielded  $^{15}\text{N}/^{14}\text{N}$  ratios (not reported here) and percentage nitrogen (‰N).

Fifty-four specimens were selected for detergent fibre analysis, chosen to incorporate dry and wet season material, taking two dry and two wet season specimens for each species where possible. In cases where the available sample was too small for analysis (< 0.5 g), several individual samples were pooled. Exposure to neutral detergent and acid detergent solutions in an ANKOM 220 Fibre Analyser yielded NDF and ADF fractions, respectively. ADL was determined by exposure of the ADF fraction to 72% (by weight)  $\text{H}_2\text{SO}_4$ . We report these data as percentage of dry matter, correcting for ash residue following furnace combustion at 525 °C over 4 h.

#### DATA ANALYSIS

Faecal  $\delta^{13}\text{C}$  values were converted to % $\text{C}_4$  intake using a dual-mixing model (Cerling *et al.* 2003; Sponheimer *et al.* 2003a), taken to represent percentage grass consumed, since virtually all grasses in Kruger Park are  $\text{C}_4$  while the overwhelming majority of other plant types are  $\text{C}_3$  (J. Codron *et al.* 2005). We assumed a diet–faeces  $^{13}\text{C}$ -discrimination of  $-0.9\text{‰}$  (Sponheimer *et al.* 2003b; D. Codron *et al.* 2005), and used means for local vegetation data to provide  $\text{C}_3$  and  $\text{C}_4$  endpoints specific to the regions and seasons included here (data from J. Codron *et al.* 2005). This approach therefore accounts for spatio-temporal variations in the carbon isotope composition of Kruger Park plants, and has been shown to yield accurate dietary estimates (within  $\pm 5\%$ ; D. Codron *et al.* 2005). Given the small error, however, diet changes from the dry to wet season are only considered significant if estimated grass intake differs by 10% or more. Comparisons of grass intake and faecal %N between browsers, grazers and mixed-feeders are carried out using analysis of variance (ANOVA) and Tukey's *post hoc* HSD. For faecal fibre data we use the nonparametric Mann–Whitney *U*-test for small sample sizes and non-normal distributions.

Relationships between diet, diet quality and morphological adaptation are based on simple linear regression models of log-transformed data. We first test the relationship between diet (percentage grass intake) and faecal proxies for diet quality (‰N, NDF, ADF and ADL), and thereafter the influence of these variables on body size and hypsodonty. Data for body size are mean female body mass (kg) reported in Skinner & Smithers (1990) and Estes (1991), and we use the hypsodonty index (HI; height : width ratio of  $\text{M}_3$  enamel crowns) of Janis (1988).

Similar approaches have been used previously to test relationships between diet, body mass and hypsodonty

(e.g. Gagnon & Chew 2000; Cerling *et al.* 2003; Sponheimer *et al.* 2003a). However, inferences may be partially constrained because accepting or rejecting a model depends solely on the significance (*P*-value) of the correlation, and only single hypotheses can be tested simultaneously (Burnham & Anderson 2001, 2002). An alternative approach is based on Kullback–Leibler information theory systems, such as Akaike's Information Criterion (AIC; Akaike 1983; Burnham & Anderson 2001, 2002). Information theory follows the concept of parsimony (simplicity), allows for testing multiple working models, and model selection is based on 'strength-of-evidence' rather than whether a given effect has statistical significance. Here we use the second-order AIC ( $\text{AIC}_c$ ) for smaller sample numbers (number of taxa < 40) based on generalized linear regression models for relationships between body mass and HI with diet and diet quality. Model selection is based on delta  $\text{AIC}_c$  ( $\Delta_i$ ) and Akaike weights ( $w_i$ ), calculated from:

$$\Delta_i = \text{AIC}_{ci} - \text{minimum AIC}_c,$$

and

$$w_i = \frac{\exp(-\Delta_i/2)}{\sum_{r=1}^R \exp(-\Delta_r/2)}$$

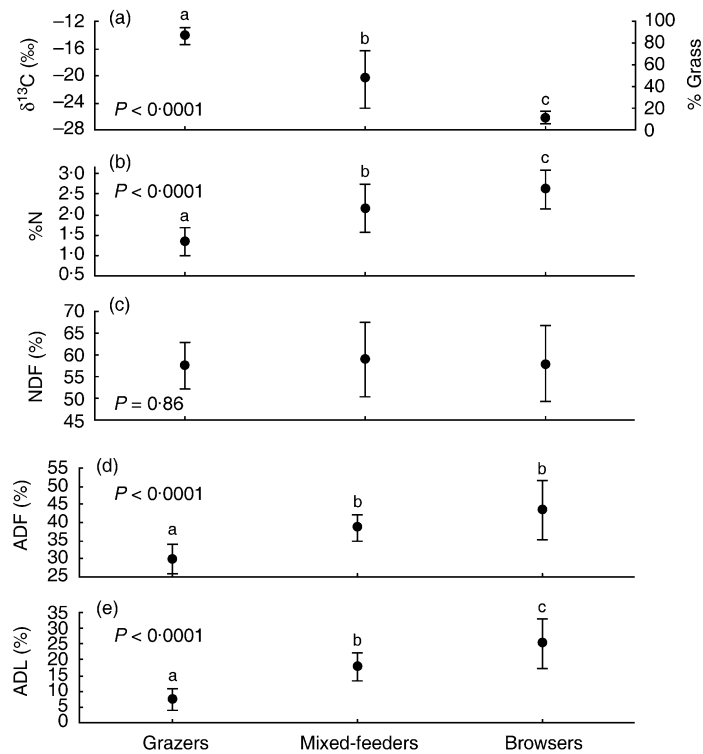
where *i* represents the candidate model, *R* the whole set of models, and *r* = 1 that the sum for all models must be 1. For  $\Delta_i < 2$ , we consider a model to be strongly supported, and  $w_i$  indicates strength of evidence, i.e. the likelihood of a candidate model having the best fit among the whole set of models. We then determine the relative importance of individual variables by summing the  $w_i$  for each parameter from all models in which it occurs (predictor weight), and by calculating the 95% confidence interval from the weighted average of each parameter ( $\theta$ ) (Burnham & Anderson 2001). This weighted average is defined as:

$$\theta = \sum w_i \theta_i$$

Variables with the largest predictor weight are considered the most important, and are taken to influence the response variable if 95% confidence limits exclude zero (Burnham & Anderson 2001, 2002). Data for dry and wet seasons are treated as separate cases, i.e. we use both a dry and a wet season mean for each species in the models to control for variations at this scale. All tests are repeated using only members of the family Bovidae so that our findings may be directly compared with previous studies on this family (e.g. Gagnon & Chew 2000; Cerling *et al.* 2003; Sponheimer *et al.* 2003a).

#### Results

As expected, faecal  $\delta^{13}\text{C}$  data are consistent with  $\text{C}_3$  in browsers (mean =  $-26.2\text{‰} \pm 0.1$  SE,  $n = 257$ ; percentage grass intake *c.* 7%),  $\text{C}_4$  in grazers ( $-14.1\text{‰} \pm 0.0$  SE,



**Fig. 1.** Faecal  $\delta^{13}\text{C}$  and estimated % grass intake (a); %N (b); NDF (c); ADF (d); and ADL (e) of browsing, mixed-feeding, and grazing ungulates in this study, ANOVA  $P$ -values are presented, and significant differences between groups ( $P < 0.05$  based on Turkey's HSD for % grass and %N, Mann–Whitney U-test for faecal fibres) are indicated with different letters (a, b, and c). Symbols depict means and bars  $\pm 1$  standard deviation (S.D.).

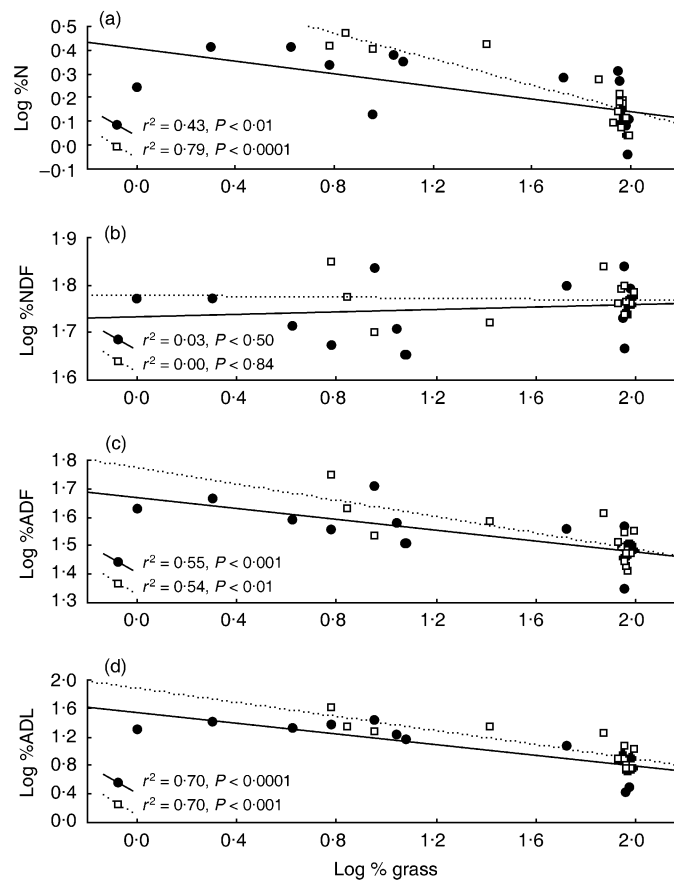
$n = 744$ ; percentage grass intake  $c. 92\%$ ), and intermediate  $\text{C}_3/\text{C}_4$  in mixed-feeders ( $-20.5 \pm 4.3\text{‰}$ ,  $n = 268$ ; percentage grass intake  $c. 48\%$ ) (Fig. 1a). Differences between means for each group are strongly significant (ANOVA  $F_{2,1266} = 3154.845$ ,  $P < 0.0001$ ; Tukey's HSD  $P < 0.0001$  for all comparisons). Faecal %N is highest for browsers ( $2.6\% \pm 0.0$  SE,  $n = 257$ ), lowest for grazers ( $1.3\% \pm 0.0$  SE,  $n = 744$ ), and intermediate for mixed-feeders ( $2.2\% \pm 0.0$  SE,  $n = 268$ ) (Fig. 1b). Again, differences between all three groups are strongly significant ( $F_{2,1266} = 941.568$ ,  $P < 0.0001$ ). By contrast, faecal NDF is similar for browsers (mean =  $58.0\% \pm 2.4$  SE,  $n = 13$ ), grazers ( $57.6\% \pm 0.9$  SE,  $n = 33$ ), and mixed-feeders ( $59.1\% \pm 3.0$  SE,  $n = 8$ ) (Mann–Whitney  $P = 0.47\text{--}0.99$ ; Fig. 1c). Faecal ADF of browsers ( $43.6\% \pm 2.3$  SE) is similar to that of mixed-feeders ( $38.5\% \pm 1.2$  SE;  $P = 0.19$ ), but grazers have lower faecal ADF than both ( $29.9\% \pm 0.7$  SE;  $P < 0.0001$ ) (Fig. 1d). Mean ADL of faeces differs between all three groups ( $P < 0.0001$ ), being highest in browsers ( $25.1\% \pm 2.2$  SE), lowest in grazers ( $7.3\% \pm 0.6$  SE), and intermediate in mixed-feeders ( $17.7\% \pm 1.6$  SE) (Fig. 1e).

Significant (i.e.  $\geq 10\%$ ) seasonal changes in diet are only apparent for mixed-feeders ( $c. 40$  compared with  $55\%$  grass intake in the dry and wet season, respectively). Seasonal differences in faecal %N are only significant for browsers (Tukey's  $P < 0.0001$ ;  $P = 0.32$  for grazers and  $0.09$  for mixed-feeders), and no seasonal changes in faecal NDF, ADF and ADL were recorded within any feeding guild (Mann–Whitney  $P$  ranged

from  $0.14$  to  $0.69$ ). There are larger seasonal changes in diet quality at species level. Mixed-feeding nyala *Tragelaphus angasii* (Gray, 1849) and grazing buffalo *Syncerus caffer* (Sparman, 1779), tsessebe *Damaliscus lunatus* (Burchell 1823) and roan antelope *Hippotragus equinus* (Desmarest, 1804) all show higher faecal %N in the wet season compared with the dry ( $F_{1,100} = 4.888$ ,  $P < 0.05$ ;  $F_{1,144} = 21.443$ ,  $P < 0.0001$ ;  $F_{1,53} = 5.624$ ,  $P < 0.05$ ; and  $F_{1,84} = 65.833$ ,  $P < 0.0001$ , respectively). Grazing warthog *Phacochoerus africanus* (Gmelin, 1788) and waterbuck *Kobus ellipsiprymnus* (Ogilby, 1833) have lower faecal %N in the wet season compared with the dry ( $F_{1,38} = 32.499$ ,  $P < 0.0001$ ; and  $F_{1,57} = 18.394$ ,  $P < 0.001$ , respectively). There are also dry-to-wet season changes in faecal fibres of some species, although sample numbers are too small for statistical comparison. Giraffe *Giraffa camelopardalis* (Linnaeus, 1758) faecal NDF, ADF and ADL increased by up to  $20\%$ , and impala *Aepyceros melampus* (Lichtenstein, 1812) and nyala faecal ADL by  $c. 5\text{--}6\%$ , from the dry to wet season, while warthog and waterbuck faecal NDF and ADF was  $c. 10\%$  higher in the wet season compared with the dry.

#### RELATIONSHIPS BETWEEN GRASS INTAKE AND DIET QUALITY

Linear regression models revealed significant negative correlations between percentage grass intake and faecal %N during both the dry ( $r^2 = 0.43$ ,  $P < 0.01$ ) and wet season ( $r^2 = 0.79$ ,  $P < 0.0001$ ) (Fig. 2a). A similar result



**Fig. 2.** Linear correlation between % grass in diet and faecal proxies for diet quality: %N (a); NDF (b); ADF (c); and ADL (d). Closed circles depict wet season means for each species with solid line representing linear fit, open squares and dashed lines represent dry season data.

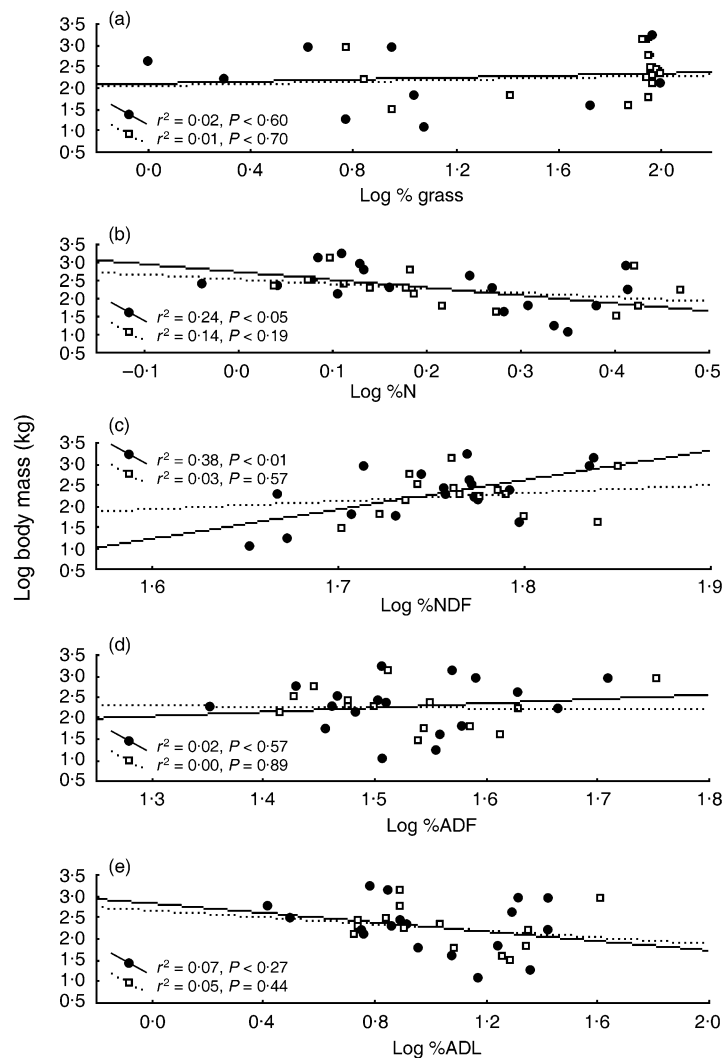
was found using only bovids (dry season  $r^2 = 0.46$ ,  $P < 0.05$ ; wet season  $r^2 = 0.80$ ,  $P < 0.001$ ). Percentage grass intake shows no significant correlation with faecal NDF (dry season  $r^2 = 0.03$ ,  $P = 0.50$ ; wet season  $r^2 = 0.00$ ,  $P = 0.84$ ; Fig. 2b), but is correlated with faecal ADF (dry season  $r^2 = 0.55$ ,  $P < 0.001$ ; wet season  $r^2 = 0.54$ ,  $P < 0.01$ ; Fig. 2c) and ADL (dry season  $r^2 = 0.70$ ,  $P < 0.0001$ ; wet season  $r^2 = 0.70$ ,  $P < 0.01$ ; Fig. 2d). Again, similar patterns were observed within the Bovidae, although the correlation between diet and faecal ADF in the wet season only approaches significance ( $r^2 = 0.02$ ,  $P = 0.68$  and  $r^2 = 0.14$ ,  $P = 0.29$  for NDF;  $r^2 = 0.65$ ,  $P < 0.01$  and  $r^2 = 0.37$ ,  $P = 0.06$  for ADF; and  $r^2 = 0.70$ ,  $P < 0.001$  and  $r^2 = 0.60$ ,  $P < 0.01$  for ADL).

The negative correlation between grass intake and faecal %N parallels the higher faecal %N of browsers compared with grazers (Fig. 1b) and expectations for higher %N of browse compared with grass (Robbins 1993; Van Soest 1994; D. Codron *et al.* 2006). Diet quality, at least in terms of crude protein content, therefore decreases with increased grass consumption. By contrast, results for faecal NDF and ADF do not reflect trends in vegetation, because grasses have far higher NDF and ADF contents than trees and forbs (Robbins 1993; Van Soest 1994; D. Codron *et al.* 2006). Thus, faecal NDF and ADF are likely influenced by higher fibre digestibility of grass cell walls (Van Soest

1994; Hummel *et al.* 2006) and/or higher fibre-digestion efficiency of grazers compared with browsers (Van Wieren 1996; Perez-Barberia *et al.* 2004). Decreasing faecal ADL with increased grass intake directly reflects the lower lignin content of grass compared with dicots, which is not surprising because digestibility of lignin is expected to be negligible (e.g. Demment & Van Soest 1985; Van Soest 1994; Van Wieren 1996). Hence, we only use faecal %N and ADL as proxies for testing influences of diet quality on morphological adaptation (Figs 3 and 4; Tables 1 and 2). Nonetheless, faecal NDF and ADF data do reveal some interesting trends, such as the positive correlation between body mass and faecal NDF in the dry season ( $r^2 = 0.36$ ,  $P < 0.01$ , Fig. 3c;  $r^2 = 0.30$ ,  $P = 0.07$  for bovids only).

#### RELATIONSHIPS BETWEEN DIET AND MORPHOLOGY

There is no significant correlation between body mass and percentage grass intake (dry season  $r^2 = 0.02$ ,  $P = 0.60$ ; wet season  $r^2 = 0.01$ ,  $P = 0.70$ ; Fig. 3a), and this persists within the Bovidae alone (dry season  $r^2 = 0.05$ ,  $P = 0.50$ ; wet season  $r^2 = 0.25$ ,  $P = 0.14$ ). In contrast, faecal %N is negatively correlated with body mass in the dry season ( $r^2 = 0.24$ ,  $P < 0.05$ ; Fig. 3b), and the correlation is stronger within the Bovidae (dry



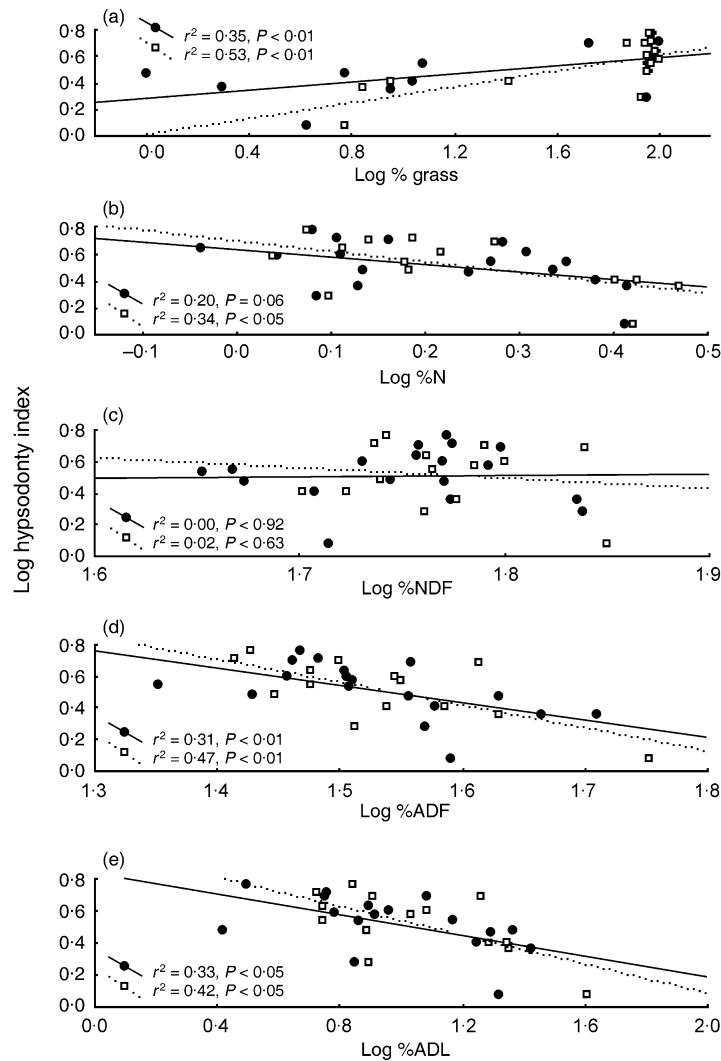
**Fig. 3.** Linear regression models for body mass with % grass intake (a) and faecal proxies for diet quality: %N (b); NDF (c); ADF (d); and ADL (e). Closed circles depict wet season means for each species with solid line representing linear fit, open squares and dashed lines represent dry season data. Body mass data are means for females from Skinner & Smithers (1990) and Estes (1991).

season  $r^2 = 0.32$ ,  $P = 0.06$ ; wet season  $r^2 = 0.36$ ,  $P = 0.07$ ). Body mass and faecal ADL are not significantly correlated (Fig. 3e), but the correlation within the Bovidae approaches significance in the dry season ( $r^2 = 0.28$ ,  $P = 0.08$ ) and is significant in the wet ( $r^2 = 0.41$ ,  $P < 0.05$ ).

Inferences based on AIC generally agree with regression models presented in Fig. 3. Notably, there is little support for a relationship between percentage grass intake and body mass ( $w_i = 0.01$ ;  $\sum w_i = 0.56$ ; 95% confidence limits =  $-0.3790$ – $0.0223$ ), but there is strong support for a relationship between body mass and faecal %N ( $w_i = 0.95$ ;  $\sum w_i = 0.56$ ; 95% confidence limits =  $-1.8528$  to  $-0.3526$ ; Table 1). Using only dry season data, %N is even more well-supported as the most important parameter influencing body mass ( $\sum w_i = 0.86$ , compared with 0.45 for percentage grass intake and 0.37 for ADL). Within the Bovidae, 95% confidence limits for the relationship between grass intake and body mass do exclude zero, but only at the third decimal place (lower limit =  $-0.0041$ ), and percentage grass is in fact the most weakly supported

model ( $w_i = 0.01$ ;  $\sum w_i = 0.50$ ). Interestingly, results for bovids only also support a relationship between faecal ADL and body mass ( $w_i = 0.18$ ;  $\sum w_i = 0.76$ ; 95% confidence limits =  $-0.8714$  to  $-0.0810$ ).

There is a positive linear correlation between HI and percentage grass intake (dry season  $r^2 = 0.35$ ,  $P < 0.01$ ; wet season  $r^2 = 0.53$ ,  $P < 0.01$ ; Fig. 4a), and the trend is even stronger within the Bovidae (dry season  $r^2 = 0.52$ ,  $P < 0.01$ ; wet season  $r^2 = 0.63$ ,  $P < 0.01$ ). HI also shows negative correlations with diet quality ( $r^2 = 0.20$ ,  $P = 0.06$  and  $r^2 = 0.34$ ,  $P < 0.05$  for %N;  $r^2 = 0.33$ ,  $P < 0.05$  and  $r^2 = 0.42$ ,  $P < 0.05$  for ADL; Fig. 4b,e). Similarly, when only bovids are considered, HI is negatively correlated with faecal %N (dry season  $r^2 = 0.37$ ,  $P < 0.05$ ; wet season  $r^2 = 0.51$ ,  $P < 0.05$ ). Multi-model inference using AIC shows strongest support for HI with percentage grass models (all species  $w_i = 0.45$ ;  $\sum w_i = 0.92$ ; 95% confidence limits =  $0.0122$ – $0.6851$ ; Bovidae only  $w_i = 0.39$ ;  $\sum w_i = 0.92$ ; 95% confidence limits =  $0.0431$ – $0.4396$ ). Percentage grass intake appears in all well-supported models (i.e. where  $\Delta_i < 2$ ), but support decreases



**Fig. 4.** Linear regression models for hypsodonty index with % grass intake (a) and faecal proxies for diet quality: %N (b); NDF (c); ADF (d); and ADL (e). Closed circles depict wet season means for each species with solid line representing linear fit, open squares and dashed lines represent dry season data. Data for the hypsodonty index of  $M_3$  are from Janis (1988).

substantially when %N and/or ADL are included ( $\sum w_i$  decreases from 0.92 to range from 0.29 to 0.45), and 95% confidence limits for %N and ADL never exclude zero. Even using only dry season data, percentage grass intake is more important than diet quality ( $\sum w_i = 0.74$ , compared with 0.31 for %N and 0.43 for ADL). The implication is that significant correlations of HI with faecal %N and ADL (Fig. 4b,e) merely record variations in %N and ADL of animals eating different amounts of grass, rather than directly reflecting changes in diet quality.

### Discussion

These results provide support for both diet type and diet quality models, in that while body mass is related to diet quality, hypsodonty is related to percentage grass consumed. It is necessary to consider the case for body mass and hypsodonty separately before attempting to integrate the functional significance of these features.

The lack of relationship between body size and percentage grass intake among Kruger Park ungulates

contradicts most predictions for increasing grass intake with increasing body size (e.g. Jarman 1974; Demment & Van Soest 1985; Gagnon & Chew 2000; Cerling *et al.* 2003), but concurs with previously published stable carbon isotope data for southern African bovids (Sponheimer *et al.* 2003a). As noted by Sponheimer *et al.* (2003a), the main reason for this is the presence of large-bodied tragelaphines such as eland *Taurotragus oryx* (Pallas, 1766) and kudu *Tragelaphus strepsiceros* (Pallas, 1766) at the  $C_3$  end of the browser/grazer spectrum. Outside the Bovidae, large-bodied browsers such as giraffe and black rhinoceros *Diceros bicornis* (Linnaeus, 1758) further diminish predictions for increasing grass intake with increased body size. In addition, our data also only include two small-bodied (< 20 kg) browser species [steenbok *Raphicerus campestris* (Thunberg, 1811) and grey duiker *Sylvicapra grimmia* (Linnaeus, 1758)], whereas studies such as Gagnon & Chew (2000) and Cerling *et al.* (2003) include several small browsers, especially duikers of the genus *Cephalophus*. Hence, the relationship between body size and



**Table 1.** Akaike's second-order information criterion (AIC<sub>c</sub>) of the regression models of ungulate body mass with diet type (percentage grass intake) and diet quality (faecal %N and faecal %ADL). Models are repeated using only members of the family Bovidae

| Model (body mass-dependent) | K | AIC <sub>c</sub> | Δ <sub>i</sub> | w <sub>i</sub> | Weighted averages |        |            |            |
|-----------------------------|---|------------------|----------------|----------------|-------------------|--------|------------|------------|
|                             |   |                  |                |                | Σ w <sub>i</sub>  | SE     | -95% conf. | +95% conf. |
| <b>All species</b>          |   |                  |                |                |                   |        |            |            |
| % grass                     | 3 | 55.50            | 7.03           | 0.01           | 0.56              | 0.1024 | -0.3790    | 0.0223     |
| %N                          | 3 | 48.90            | 0.44           | 0.29           | 0.95              | 0.3827 | -1.8528    | -0.3526    |
| %ADL                        | 3 | 53.65            | 5.18           | 0.03           | 0.33              | 0.2143 | -0.5752    | 0.2648     |
| % grass, %N                 | 4 | 48.46            | 0.00           | 0.37           |                   |        |            |            |
| % grass, %ADL               | 4 | 55.04            | 6.57           | 0.01           |                   |        |            |            |
| %N, %ADL                    | 4 | 50.78            | 2.31           | 0.12           |                   |        |            |            |
| % grass, %N, %ADL           | 5 | 49.96            | 1.50           | 0.17           |                   |        |            |            |
| Model average               |   |                  |                |                |                   | 0.3456 | 0.8122     | 2.1668     |
| <b>Bovidae only</b>         |   |                  |                |                |                   |        |            |            |
| % grass                     | 3 | 29.12            | 7.01           | 0.01           | 0.50              | 0.0916 | -0.3633    | -0.0041    |
| %N                          | 3 | 23.24            | 1.13           | 0.17           | 0.72              | 0.3638 | -1.5195    | -0.0935    |
| %ADL                        | 3 | 23.17            | 1.06           | 0.18           | 0.76              | 0.2016 | -0.8714    | -0.0810    |
| % grass, %N                 | 4 | 24.84            | 2.73           | 0.08           |                   |        |            |            |
| % grass, %ADL               | 4 | 24.18            | 2.06           | 0.11           |                   |        |            |            |
| %N, %ADL                    | 4 | 23.26            | 1.15           | 0.17           |                   |        |            |            |
| % grass, %N, %ADL           | 5 | 22.11            | 0.00           | 0.30           |                   |        |            |            |
| Model average               |   |                  |                |                |                   | 0.3117 | 1.0669     | 2.2888     |

Italics depict parameters for which 95% confidence limits exclude zero. *K* = number of parameters; Δ<sub>i</sub> = delta AIC<sub>c</sub>; w<sub>i</sub> = Akaike weight; SE = standard error.

**Table 2.** Akaike's second-order information criterion (AIC<sub>c</sub>) of the regression models of ungulate hypsodonty index with diet type (percentage grass intake) and diet quality (faecal %N and faecal %ADL). Models are repeated using only members of the family Bovidae

| Model (HI-dependent) | K | AIC <sub>c</sub> | Δ <sub>i</sub> | w <sub>i</sub> | Weighted averages |      |            |            |
|----------------------|---|------------------|----------------|----------------|-------------------|------|------------|------------|
|                      |   |                  |                |                | Σ w <sub>i</sub>  | SE   | -95% conf. | +95% conf. |
| <b>All species</b>   |   |                  |                |                |                   |      |            |            |
| % grass              | 3 | -32.97           | 0.00           | 0.45           | 0.92              | 0.17 | 0.0122     | 0.6851     |
| %N                   | 3 | -25.23           | 7.74           | 0.01           | 0.29              | 0.53 | -1.0542    | 1.0342     |
| %ADL                 | 3 | -28.80           | 4.17           | 0.06           | 0.38              | 0.27 | -0.7096    | 0.3558     |
| % grass, %N          | 4 | -30.99           | 1.98           | 0.17           |                   |      |            |            |
| % grass, %ADL        | 4 | -31.40           | 1.56           | 0.21           |                   |      |            |            |
| %N, %ADL             | 4 | -27.79           | 5.17           | 0.03           |                   |      |            |            |
| % grass, %N, %ADL    | 5 | -29.40           | 3.56           | 0.08           |                   |      |            |            |
| Model average        |   |                  |                |                |                   | 0.51 | -2.0503    | -0.0579    |
| <b>Bovidae only</b>  |   |                  |                |                |                   |      |            |            |
| % grass              | 3 | -43.13           | 0.00           | 0.39           | 0.92              | 0.10 | 0.0431     | 0.4396     |
| %N                   | 3 | -38.87           | 4.26           | 0.05           | 0.45              | 0.34 | -1.0879    | 0.2440     |
| %ADL                 | 3 | -34.83           | 8.31           | 0.01           | 0.30              | 0.19 | -0.2572    | 0.4830     |
| % grass, %N          | 4 | -42.33           | 0.81           | 0.26           |                   |      |            |            |
| % grass, %ADL        | 4 | -41.22           | 1.91           | 0.15           |                   |      |            |            |
| %N, %ADL             | 4 | -37.50           | 5.63           | 0.02           |                   |      |            |            |
| % grass, %N, %ADL    | 5 | -40.70           | 2.43           | 0.12           |                   |      |            |            |
| Model average        |   |                  |                |                |                   | 0.32 | -1.6329    | -0.3740    |

Italics depict parameters for which 95% confidence limits exclude zero. *K* = number of parameters; Δ<sub>i</sub> = delta AIC<sub>c</sub>; w<sub>i</sub> = Akaike weight; SE = standard error.

grass intake is likely only to hold when animals below 20 kg are considered, but beyond this range, there appears to be no relationship between body size and grass consumption. Some species not included here also do not conform to general predictions. Oribi *Ourebia ourebi*

(c. 14 kg) are expected to be a predominantly grazing species (Owen-Smith 1997); African elephants (up to 6000 kg) are primarily browsers in most savanna habitats (Cerling, Harris & Leakey 1999); and small-bodied grazers, e.g. *Antidorcas bondi*, were also

prominent in the Pleistocene (Brink & Lee-Thorp 1992).

The relationship between body size and diet quality agrees with expectations that smaller species require higher energy yields from their food in order to maintain higher metabolic rates (Bell 1970; Jarman 1974; Demment & Van Soest 1985; Owen-Smith 1988). This may appear contradictory to the lack of support for significant influence of diet type, because the lower protein : fibre ratios of grass compared with browse-based foods is widely interpreted as a reflection of poorer diet quality in the former (Jarman 1974; Demment & Van Soest 1985; Hofmann 1989; Gagnon & Chew 2000). However, woody plants are more lignified and contain a higher proportion of digestion-inhibiting phenols and other secondary compounds than do grasses (Robbins 1993; Van Soest 1994; D. Codron *et al.* 2006). Hence, fibre digestibility of grasses is higher than that of browse, and overall metabolizable energy yields of the two food groups may in fact be higher in grass, or at least similar (Gordon & Illius 1996; Van Wieren 1996; Owen-Smith 1997; D. Codron *et al.* 2006; Hummel *et al.* 2006).

Some caution should be observed when interpreting faecal %N as a direct measure of diet quality. The relationship between dietary and faecal %N, especially in browsers, is complicated by protein-precipitating effects of dietary tannins, and nitrogen derived from sloughed endogenous materials and gut microbes (Robbins *et al.* 1987; Van Soest 1994). However, support for models relating body mass to faecal %N persisted in spite of (1) variations in percentage grass intake, and (2) the negative correlation between grass intake and faecal %N.

Faecal ADL provides another proxy for diet quality because it appears not to be influenced by variations in fibre digestibility, consistent with predictions that lignin is virtually undigestible by microbial fermentation (Robbins 1993; Van Soest 1994). The importance of diet quality for body size is substantiated by well-supported models of increasing faecal ADL, i.e. decreasing diet quality, with increased body size, at least within the Bovidae. Our data also reveal a trend of increasing faecal NDF with increased body size during the dry season, but it is unclear whether this represents decreases in diet quality or differential digestion of NDF by species of different body sizes.

Overall, it appears that larger animals consume relatively poorer quality foods regardless of diet type (see also Gordon & Illius 1994, 1996). Decreased diet quality with increasing body size complements expectations that fibre-digestion efficiency increases with body size (Owen-Smith 1988; Illius & Gordon 1992; Gordon & Illius 1994, 1996; Robbins *et al.* 1995). In principle, larger animals are predicted to have longer digesta retention times than smaller species, allowing for more complete microbial fermentation. Gordon & Illius (1996) hypothesized that such adaptations enable larger animals to cope with poor quality diets and

thereby avoid competition with smaller species by having a wider resource-tolerance range, especially during limiting periods. This assertion is supported by data presented here, because the relationships between body mass and faecal %N (and NDF) were strongest during the dry season. During less limiting periods (i.e. the wet season), species of all sizes appear to consume a similar range of diet qualities.

While body size was not related to diet type, our data suggest that hypsodonty increases with increasing reliance on grass. This finding is in agreement with numerous other studies (Janis 1988; Perez-Barberia & Gordon 2001; Williams & Kay 2001), including those using carbon isotope evidence (Cerling *et al.* 2003; Sponheimer *et al.* 2003a). In this instance we therefore expect diet type rather than diet quality to be the primary mechanism for diversification. However, hypsodonty (increased enamel volume) is predicted to be an adaptation to resist tooth-wear caused by the higher silica and exogenous grit content of grass compared with browse (Janis 1988). Thus, one might argue that hypsodonty is, in fact, related to diet quality, i.e. abrasive properties of foods consumed. Further, available data for hypsodonty do portray some potential anomalies if feeding style is interpreted as the only variable of importance. For example, Janis (1988) ascribed similar HI values to mixed-feeding impala (4.89) and grazing alcelaphines such as blue *Connochaetes taurinus* (4.94) (Burchell 1823) and black wildebeest *C. gnou* (4.75) (Zimmerman 1780). The close relationship between these taxa (impala are considered basal to, or even members of, the Alcelaphini; Gentry 1978; Janis 1988) may indicate phylogenetic retention of character traits as a complicating factor. Perez-Barberia & Gordon (2001), however, found that molar tooth height consistently reflected feeding style even after the effects of phylogenetic relationships between taxa were controlled for statistically, but also only after body size was taken into account. The latter result refers back to body size and diet quality as the more significant factor. Future studies should endeavour to contrast relationships between HI and percentage grass intake with direct correlations between HI and measures of abrasiveness of diet, e.g. variations in silica intake.

#### COMPARISON WITH OTHER MODELS

It is often accepted that diet type and quality models for ungulate diversification are in many ways complementary, because larger animals with lower quality diets are expected to consume more grass than smaller species. Hofmann (1989), however, denied a connection between dietary adaptation and body size. The results of our study are consistent with Hofmann's (1989) conclusion that adaptations to diet type are not related to body size. But, our results emphasize the importance of diet quality, and its implications for body size as a fundamental nutritional adaptation in ungulates.

Further reconciliation between diet type and diet quality models is necessary.

Our interpretation that diet quality drives morphological and physiological adaptations in ungulates, regardless of the type of foods consumed, concurs with some studies (e.g. Gordon & Illius 1994, 1996; Robbins *et al.* 1995), but is in many ways contradictory to most recent tests and reviews of these models (Van Wieren 1996; Owen-Smith 1997; Clauss & Lechner-Doll 2001; Perez-Barberia *et al.* 2004; Clauss, Hummel & Streich 2006). All of the latter support predictions for increased fibre digestion efficiency with increased grass consumption and advocate diet type as the primary mechanism for diversification. This may explain why, in our study, faecal NDF did not correlate well with percentage grass intake; faecal NDF in grazers, which eat foods with relatively higher NDF content, was as low as that of browsers, possibly because grazers digested greater proportions of NDF consumed.

One possible explanation for the apparent disparity between our findings and most recent suggestions is that adaptations to diet quality may be based on differences in the physical, rather than biochemical, properties of browse and grass (Clauss *et al.* 2003). Recent studies have demonstrated differences in particle size into which browse and grass are broken down in the digestive tract (Clauss, Lechner-Doll & Streich 2002), formation of a stratified, fibrous raft by grasses in the rumen (Clauss *et al.* 2003), and differences in fluid dissociation (Clauss *et al.* 2006), and these properties have been associated with differences in digestive morphophysiology between browsers and grazers. However, the authors recognize constraints to their studies in that they could not control for the type and nutritional quality of food ingested, the number of species for which data are available was small, and information on the physicomechanical properties of browse and grass is limited. None the less, plant physical properties may be a common factor underlying variations in both fibre digestion (Clauss *et al.* 2003) and hypsodonty, the latter in terms of abrasiveness of the material. Further tests for relationships between plant physical properties and functional morphology may yield universal solutions to diet type and diet quality models.

### Conclusions

Predictions for the effects of diet type and diet quality on ungulate ecological diversity, based on evidence from feeding trials, statistical models, and/or collating data from a wide body of literature sources, are often incongruent with events in free-ranging situations. Intraspecific changes in diet and diet quality over different seasons and/or habitats also influence model testing, and some species have even been shown to achieve different dry matter digestibilities in response to changes in diet quality through the seasonal cycle (Meissner, Pieterse & Potgieter 1996; Bodenstern,

Meissner & van Hoven 2000). Only Owen-Smith (1997) attempted to integrate seasonal variations when assessing differences between feeding styles, but he recognized the paucity of data available for nutritional variations in most taxa. In combining carbon isotope data with faecal proxies for diet quality, we have made a preliminary attempt to bridge these gaps. If we are to properly understand the functional significance of diet type and diet quality in ungulates, nutritional physiologists and wildlife ecologists will need to work together to develop methodological and statistical approaches in order to maximize benefits of both types of research.

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## Supplementary material

The following supplementary material is available for this article.

**Table S1.** Mean faecal  $\delta^{13}\text{C}$ , %N and fibre content for Kruger Park ungulates

This material is available as part of the online article from: <http://www.blackwell-synergy.com/doi/full/10.1111/j.1365-2656.2007.01222.x>

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**Table S1.** Mean faecal  $\delta^{13}\text{C}$ , %N, and fibre content for Kruger Park ungulates.

Number of samples pooled for fibre analysis is presented as the number comprising each specimen analysed. Dry season = April to September, wet season = October to March. Landscape key: NB = northern basalts, SB = southern basalts, NG = northern granites, SG = southern granites, PM = Punda Maria.

| Species                         | Region/<br>season | n  | $\delta^{13}\text{C}_{\text{VPDB}} (\%)$ |      | %N   |      | n | Number<br>pooled | Mean (%) |      |      |
|---------------------------------|-------------------|----|--|------|------|------|---|------------------|----------|------|------|
|                                 |                   |    | Mean                                     | S.E. | Mean | S.E. |   |                  | NDF      | ADF  | ADL  |
| <b>Browsers</b>                 |                   |    |  |      |      |      |   |                  |          |      |      |
| <i>Diceros bicornis</i>         | SB Dry            | 9  | -26.1                                    | 0.1  | 1.3  | 0.1  | 1 | 6                | 68.4     | 51.2 | 26.8 |
| <i>Giraffa camelopardalis</i>   | NB Dry            | 62 | -26.4                                    | 0.1  | 2.6  | 0.0  | 2 | 1, 1             | 51.8     | 39.1 | 20.8 |
|                                 | NB Wet            | 56 | -26.0                                    | 0.1  | 2.6  | 0.0  | 2 | 1, 1             | 70.8     | 56.6 | 40.6 |
| <i>Raphicerus campestris</i>    | NG Dry            | 7  | -25.3                                    | 1.1  | 2.2  | 0.2  | 1 | 6                | 44.9     | 32.2 | 14.8 |
| <i>Sylvicapra grimmia</i>       | SG Dry            | 7  | -26.2                                    | 0.2  | 2.2  | 0.1  | 1 | 7                | 47.1     | 36.0 | 23.1 |
| <i>Taurotragus oryx</i>         | NB Dry            | 2  | -27.4                                    | 0.1  | 1.8  | 0.0  | 1 | 1                | 59.0     | 42.7 | 19.8 |
| <i>Tragelaphus scriptus</i>     | SG Wet            | 7  | -26.3                                    | 0.6  | 2.5  | 0.1  | 1 | 7                | 50.3     | 34.6 | 19.4 |
| <i>Tragelaphus strepsiceros</i> | PM Dry            | 48 | -26.7                                    | 0.1  | 2.6  | 0.1  | 2 | 1, 1             | 59.4     | 46.3 | 26.5 |
|                                 | PM Wet            | 59 | -25.9                                    | 0.1  | 3.0  | 0.0  | 2 | 4, 5             | 60.0     | 43.0 | 23.1 |
| <b>Mixed-feeders</b>            |                   |    |  |      |      |      |   |                  |          |      |      |
| <i>Aepyceros melampus</i>       | NB Dry            | 88 | -19.8                                    | 0.3  | 1.9  | 0.1  | 2 | 1, 1             | 62.9     | 36.2 | 12.1 |
|                                 | NB Wet            | 78 | -16.6                                    | 0.2  | 1.9  | 0.0  | 2 | 1, 1             | 69.1     | 41.0 | 18.3 |
| <i>Tragelaphus angasii</i>      | PM Dry            | 43 | -25.4                                    | 0.5  | 2.4  | 0.1  | 2 | 1, 2             | 51.3     | 38.0 | 17.8 |
|                                 | PM Wet            | 59 | -23.2                                    | 0.5  | 2.7  | 0.1  | 2 | 4, 5             | 53.1     | 38.8 | 22.5 |
| <b>Grazers</b>                  |                   |    |  |      |      |      |   |                  |          |      |      |
| <i>Ceratotherium simum</i>      | SB Dry            | 9  | -14.2                                    | 0.5  | 1.3  | 0.1  | 1 | 15               | 58.8     | 32.1 | 6.1  |
| <i>Connochaetes taurinus</i>    | NB Dry            | 60 | -14.4                                    | 0.1  | 1.4  | 0.1  | 2 | 1, 1             | 57.3     | 29.0 | 5.7  |
|                                 | NB Wet            | 55 | -14.7                                    | 0.1  | 1.4  | 0.0  | 2 | 1, 1             | 61.8     | 31.6 | 8.3  |
| <i>Damaliscus lunatus</i>       | NB Dry            | 14 | -13.2                                    | 0.2  | 1.3  | 0.1  | 2 | 2, 1             | 59.6     | 30.5 | 5.8  |
|                                 | NB Wet            | 41 | -14.0                                    | 0.2  | 1.5  | 0.1  | 2 | 1, 1             | 55.1     | 26.3 | 5.5  |
| <i>Equus burchellii</i>         | NB Dry            | 59 | -14.2                                    | 0.1  | 1.2  | 0.1  | 2 | 4, 1             | 59.2     | 29.6 | 3.6  |
|                                 | NB Wet            | 70 | -14.2                                    | 0.1  | 1.2  | 0.0  | 2 | 1, 1             | 55.4     | 27.0 | 7.4  |
| <i>Hippopotamus amphibius</i>   | SB Dry            | 10 | -13.6                                    | 0.4  | 1.2  | 0.1  | 1 | 8                | 68.9     | 37.1 | 7.0  |
|                                 | SG Wet            | 5  | -15.5                                    | 0.5  | 1.3  | 0.1  | 1 | 5                | 57.8     | 32.6 | 7.9  |
| <i>Hippotragus equinus</i>      | NB Dry            | 47 | -13.6                                    | 0.1  | 0.9  | 0.0  | 2 | 1                | 57.2     | 31.9 | 8.2  |
|                                 | NB Wet            | 39 | -13.5                                    | 0.2  | 1.3  | 0.0  | 2 | 1                | 57.9     | 30.0 | 5.7  |
| <i>Hippotragus niger</i>        | SG Dry            | 31 | -13.1                                    | 0.1  | 1.1  | 0.0  | 1 | 13               | 62.1     | 32.4 | 8.3  |
|                                 | SG Wet            | 59 | -13.1                                    | 0.1  | 1.1  | 0.0  | 1 | 20               | 61.1     | 35.5 | 10.9 |
| <i>Kobus ellipsiprymnus</i>     | NB Dry            | 20 | -15.0                                    | 0.3  | 1.9  | 0.1  | 2 | 3, 3             | 46.6     | 22.6 | 7.3  |
|                                 | NB Wet            | 39 | -14.5                                    | 0.2  | 1.5  | 0.0  | 2 | 1, 1             | 58.3     | 30.1 | 6.7  |
| <i>Phacochoerus africanus</i>   | NB Dry            | 11 | -14.9                                    | 0.3  | 2.0  | 0.0  | 2 | 1, 1             | 53.9     | 28.9 | 10.2 |
|                                 | NB Wet            | 29 | -14.4                                    | 0.2  | 1.6  | 0.0  | 2 | 1, 1             | 63.3     | 35.3 | 13.5 |
| <i>Syncerus caffer</i>          | NB Dry            | 73 | -14.7                                    | 0.1  | 1.4  | 0.0  | 2 | 1, 1             | 55.6     | 27.0 | 3.7  |
|                                 | NB Wet            | 73 | -14.4                                    | 0.1  | 1.5  | 0.0  | 2 | 1, 1             | 55.0     | 28.1 | 7.9  |

n = number of samples; S.E. = standard error