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The potential and pitfalls of using simple dental metrics to infer the diets of African antelopes (Mammalia: Bovidae)

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The use of mesowear to infer diets of extinct species is fast becoming widespread in palaeoecological studies. Nevertheless, traditional mesowear analyses suffer from a specimen number limitation, in that a minimum number of specimens identified to the species level is necessary to make accurate dietary predictions. This is problematic in many fossil African antelope (Mammalia: Bovidae) assemblages, where isolated teeth cannot always be assigned to species. Here we explore the possibility of using simple dental metrics to predict diets on the basis of individual teeth as well as gnathic rows using linear discriminant function analyses. We find that browsers are accurately classified at both the individual and species levels, across all models and tooth positions. Mixed feeders and grazers are classified accurately only sometimes, and this is probably a reflection of the more limited sample size of larger bodied species in our study. Body size was a highly significant predictor of the inaccurate classifications obtained in our models, with larger bodied species tending to grazing classifications and smaller bodied species browsing classifications. Nevertheless, the models correctly classify the majority of specimens we examined to their correct trophic group, as determined through stable isotope analyses or as defined through the literature. The methods outlined hold some promise for determining the diets of isolated fossil specimens unassigned to species in a simple manner and, when used in conjunction with other palaeodietary and palaeoecological proxies, may help determine palaeoenvironments more accurately.

Keywords: mesowear, palaeodiet, palaeoecology, tooth wear.

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INTRODUCTION

Bovid gnathic elements (isolated teeth, tooth-bearing and edentulous mandibles and maxillae) are amongst the most commonly recovered specimens in African late Cenozoic palaeontological assemblages. These elements are directly involved in food processing and are most often recovered as complete or near-complete elements. Several different proxies have emerged to predict diets of African bovids on the basis of their teeth, including stable isotope biogeochemistry, craniodental morphology, microwear analysis, and, increasingly, mesowear studies (Janis 1988, 1990; 1995; Cerling *et al.* 1997; Lee-Thorpe *et al.* 2007; Ungar *et al.* 2007; Stynder 2009; Louys *et al.* 2011; Scott 2012). Bovid teeth are thus an important source of palaeoecological data about the assemblages under investigation, as the trophic capacity of the local environment can be inferred on the basis of the abundance of particular diet types within a related group of taxa (e.g. Andrews *et al.* 1979; Vrba 1980; Faith 2013).

Mesowear analyses are a cheap, effective and accurate means of assessing the palaeodiets of fossil herbivore species, including those of African bovids. Mesowear is the cumulative dental wear an animal experiences during its lifetime. Two types of wear are commonly identified. Attritional wear is the formation of wear facets on the tooth through tooth-on-tooth contact and amongst mammalian herbivores is most commonly associated with a browse-dominated diet. Abrasive wear occurs through tooth-on-food contact and is generally indicative of grazing (Hillson 2005). The relative proportions of these two distinctive tooth wear patterns on molars, assessed by a simple visual examination, typically of the M2, can be used to determine whether an animal's diet was predominately browsing or grazing. Two qualitative variables are scored (Fortelius & Solounias 2000). The first (cusp shape) describes the relative sharpness of the sharpest buccal cusp, which can be sharp, round or blunt; the second (occlusal relief) describes the relative height of the valley between the two cusps examined for sharpness, scored as either high or low. The percentages of these two variables are calculated from a number of specimens within a species (preferably $n > 20$). The unknown species' diets can be accurately assessed as browsing,

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grazing or mixed feeding by comparing the species-averaged score (either as raw percentages or converted to a single univariate score) with a set of 27 'typical' modern species (e.g. Stynder 2009, 2011; Blondel *et al.* 2010; Faith 2011; Faith *et al.* 2011). This type of analysis correctly classified the diet of 91% (30 of 33) extant African Bovidae species examined (Louys *et al.* 2011).

Mesowear analysis has limitations, particularly when applied to fragmentary remains. First, specimens must be identified to a species. The most taxonomically informative features of bovid species are horn cores, not teeth. Individual antelope teeth might be reasonably assigned to genus or tribe, but unless specimens are associated with diagnostic cranial elements, it is difficult to identify them to species with confidence. Many fossil bovid dental elements do not have identification to species, hampering palaeospecies-level calculations of the average incidences of sharpness of cusps and occlusal height. A further limitation of mesowear analysis is that it requires a sufficient number of specimens per species to be analysed, in order for the mesowear signal to 'stabilize'. Fortelius & Solounias (2000) strongly advocated a sample size over 20, with an absolute minimum of five specimens per species; however fewer than five has been used by some researchers (e.g. Stynder 2009). Finally, the mesowear method was designed for use on the upper second molar (M2) only. While studies have extended this to other molar positions in equids (e.g. Kaiser & Fortelius 2003; Kaiser & Solounias 2003) and African bovids (Louys *et al.* 2011), for the latter group the M2 remains the best model available (Louys *et al.* 2011, 2012). Moreover, substituting a different molar for M2s is likely to give erroneous results (Louys *et al.* 2011). For any given fossil assemblage, these constraints limit application of the traditional mesowear method to only a small proportion of available specimens. For example, in our February 2010 survey of all Olduvai bovid specimens then housed in the National Museum of Kenya, Nairobi, only one species (*Parmularis altidens*; $n = 5$) had sufficiently numerous, well-preserved undamaged M2s necessary to make a confident mesowear analysis.

This study explores a taxon-free method to extend gross dental analysis to isolated bovid molars that cannot be confidently assigned to species. Isolated molars are a common fossil resource which can be used to support environmental reconstructions of palaeontological sites in conjunction with other palaeoecological proxies. In keeping with the philosophy of the mesowear method, we employ a small number of measurements that are quick and simple to take, and that can be applied to a range of molar gnathic positions across all African bovid species. Multivariate models are developed based on individual teeth as well as tooth rows. We assess the success of these models across different teeth, trophic groups, species, body size, and dietary classifications.

MATERIALS

Complete and incomplete mandibular and maxillary fragments as well as isolated teeth belonging to extant members of the Bovidae, housed in the Natural History Museum (BMNH) London, Royal Museum for Central Africa (RMCA), Tervuren, and Musée d'Histoire Naturelle (MHNP), Paris, were included in the analyses. A total of 573 modern specimens were originally measured. Specimens with broken or damaged teeth or missing measurements, and old and juvenile specimens (assessed via eruption sequences and degree of dental wear, *cf.* Fortelius & Solounias 2000), were subsequently excluded such that 299 modern adult specimens (42 species) yielding lower molar dimensions and 388 modern specimens (48 species) yielding upper molar dimensions were analysed (some individuals yielded both upper and lower measurements). Sample size was not equally distributed across all taxa, body sizes, or trophic groups due to historical, geographical or curatorial biases in museum collections. We avoided collecting from captive specimens, and all specimens examined with locality information available represented wild-caught specimens. Approximately half the extant sample was not sexed, and of those that were, distribution was roughly equal between males and females. In order to maximize sample size, and because sex is unlikely to be known for fossil specimens, sex was pooled in the analyses.

METHODS

Linear measurements

Four measurements for each molar (Fig. 1) were taken by a single observer (J.L.) using digital callipers interfaced to a laptop computer at 0.5 mm of precision. The left side was preferred; however, if unavailable or damaged measurements were taken on the right side. While crown height may be subjected to a certain amount of age-related variation, even amongst exclusively adult specimens, it was included amongst our measurements because of the strong correlation that exists between crown height and diet (e.g. Janis 1995; Mendoza & Palmqvist 2007; Raia *et al.* 2010). Unless extremely old individuals are examined, the large, evolutionarily-driven differences differentiating many grazing and browsing bovid species will be perceptible both quantitatively and qualitatively.

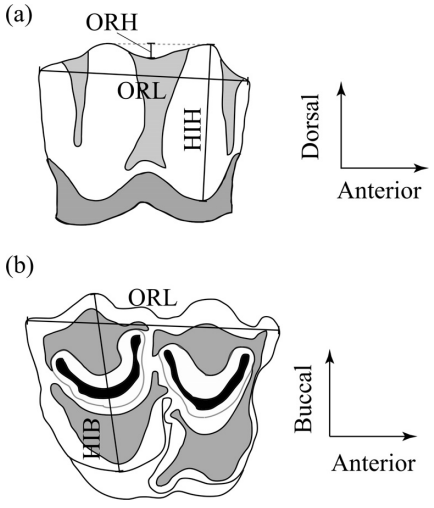


Figure 1. Representative bovid upper molar, showing measurements taken. ORH: occlusal relief height; ORL: tooth length; HIH: crown height; HIB: tooth breadth.

Dietary classification

Gagnon & Chew (2000) identified six discrete dietary strategies for African bovids: obligate grazers (defined by a diet of >90% monocots), variable grazers (60–90% monocots), browser-grazer intermediates (30–70% dicot and monocots, <20% fruits), generalists (>20% all food types), browsers (>70% dicots), and frugivores (>70% fruits, few or no monocots). These were based on an extensive literature survey and subsequent cluster analysis. For the present study, species were classified into one of three dietary categories, simplified from the six-category system of Gagnon & Chew (2000). Bovids were classified as browsers (including frugivores and browsers), mixed feeders (generalists and browser-grazer intermediate), and grazers (variable and obligate grazers) (*cf.* Raia *et al.* 2010). This classification scheme follows that used by Louys *et al.* (2011), and allows for comparability with that study.

The diets of a subset of the examined specimens were independently assessed through carbon stable isotopic analysis to examine whether the broad dietary classifications used to construct the linear discriminant analyses (LDAs) resulted in misclassifications. Carbon stable isotopes in body tissues of herbivores reflect the relative proportions of leaves and grasses in their diet (see review in Ehleringer & Monson 1993). C3 plants (largely browse) have a δ^{13}C values ranging from –32‰ in closed understorey canopy conditions to –21‰ in more open environments, while C4 plants (including many tropical grasses) can range from –21‰ to –9‰ (e.g. Cerling *et al.* 1999). The isotopic analyses were described in detail by Louys *et al.* (2012), and the δ^{13}C values they provided are used here. Briefly, at least 1 g of hair was extracted from the pelt of a subset of specimens whose diets are reconstructed using the LDAs developed in this study. Cleaned hair samples were weighed into tin capsules and analysed for their carbon stable isotopic composition by continuous flow isotope ratio mass spectrometry using a Sercon 20/22 IRMS coupled to a Sercon GSL sample combustion device using Helium carrier gas. Sample data were reported in standard delta per mil notation (δ ‰) relative to V-PDB and a 3.2‰ hair fractionation adjustment was applied (*cf.* Sponheimer *et al.* 2003). The results were converted to % C4 in diet using a two end-member equation, where –32‰ δ^{13}C is considered a purely browsing diet and –9‰ δ^{13}C a purely grazing diet (see above). In this analysis, specimens with less than 30% C4 in their diets were considered browsers, those with more than 70% grazers, and any specimens falling in between considered mixed feeders. Carbon isotope values were compared to the classifications provided by the LDAs for each specimen where both hair samples and undamaged molars were present (n = 75 for lowers, n = 86 for uppers). Comparisons between the results of the LDAs and the isotope record were made. Specimens where the median dietary classification across all models was different from the dietary classification judged according to the reduced Gagnon & Chew (2000) dietary scheme were compared with their actual diets as calculated from the carbon isotopic record. The proportions of misclassifications made regardless of dietary classification scheme used (i.e. either the reduced Gagnon & Chew (2000) or the stable isotope classifications) were calculated. The Gagnon & Chew (2000) scheme is not strictly consistent with stable carbon isotope values since δ^{13}C values reflect only C4 monocots in the diet and not all plants consumed.

Analyses

Sixteen separate linear discriminant analyses (LDAs) were undertaken using IBM SPSS Statistics version 20. Each molar type was analysed independently, resulting in six separate models. We also ran portions of the molar row as independent analyses, producing eight additional models. So for each upper and lower dental row we analysed: (i) the first and second molars; (ii) the first, second, and third molars; (iii) the first and third molars; and (iv) the second and third molars. Finally, we ran two separate models assuming unknown tooth type. For the upper tooth row this included all three molars, whereas for the lower molars this included only the m1 and m2, because the lower third molar bears three lophs and can thus be identified even by inexperienced observers. Each individual molar, depending on the extent of its associated dentition, was thus subject to up to five different LDAs. We interpreted the accuracy of each LDA on the basis of the percentage of correctly classified specimens after cross-validation (jackknifed values; *cf.* Kovarovic *et al.* 2011). Diet classifications for each specimen were tabulated, with browsers given a classification of 1, mixed 2, and grazers 3. Average (median and mean) classifications for each species were calculated across all models and specimens. In cases where classifications were split between browsers and mixed feeders, a median classification score of 1.5 was returned, and when split between mixed and grazing 2.5.

The relationship between shared phylogenetic history and dietary classification was investigated by mapping the median classification scores of all models for each species onto a phylogenetic tree of the Bovidae. This tree was adapted from Price *et al.* (2005), with the addition of *Oryx beisa* in an unresolved trichotomy with *O. gazella* and *O. leucoryx*. Species included by Price *et al.* (2005) in their phylogeny but not examined in this study were removed and the corresponding branches collapsed, so only the topologies of the species used here are displayed. Upper and lower molars were examined separately. Species were not uniformly represented across upper and lower dentitions, so the corresponding topologies differed slightly.

Raw measurements were used in statistical analyses as initial testing on variables produced lower classification accuracies when the variables were log-transformed. Although using raw measurements incorporates significant size signal in the models, the consensus view in such analyses is that size is an important ecological attribute that should not be ignored or mitigated when attempting reconstructions in a 'taxon-free' environment (DeGusta & Vrba 2003, 2005; Louys *et al.* 2013; Meloro *et al.* 2013). Nevertheless, we examined the impact of body size on our analyses and model accuracy *post hoc* by examining the

relationships between proportion of correct classifications and body mass of each species (body mass data sourced from Gagnon & Chew 2000), and by examining the effects of removing body size from our models.

RESULTS

Upper molars

All eight upper molar LDA models produced statistically significant ($P < 0.0001$) Wilks' lambda values (Table 1). Bootstrap and jackknifed classification values were all better than would be expected if each specimen had an equal chance of being assigned to one of the three dietary categories (Table 1). The worst performing model was the first upper molar, with a jackknifed classification rate of 60.6%. The best performing model was the upper second and third molar combination, with a jackknifed classification rate of 78.1%.

The majority of upper molar specimens from browsing taxa were correctly classified across all cases (Fig. 2), with 81% of species correctly classified on the basis of median classification score. Seven (of 16) browsing species were consistently classified as browsers across all models (Table 2, Fig. 3A). Five of the remaining species had more than 50% of the cases produce browsing classifications. *Cephalophus silvicultor* and *Taurotragus derbianus* were overwhelmingly missclassified as grazers. Finally, *Tragelaphus eurycerus* was classified as a mixed feeder, an identical result to the lower molar analyses. The majority of mixed-feeding specimens examined were misclassified as browsers across all models (Fig. 4). Only one species, *Aepyceros melampus*, had all cases correctly classified to mixed (Table 3, Fig. 3C; $n = 3$; four cases). Four of 12 (33%) mixed-feeding species produced a correct median classification of 2. In addition to *Ae. melampus*, *Antidorcas marsupialis*, *Gazella soemmerringi*, and *Tragelaphus strepsiceros* were classified as mixed feeders, although only in the latter three species were ≥50% given a mixed-feeding classification.

Table 1. Wilk's lambda, bootstrap and jackknife classification values for the 16 models examined; for all values $P < 0.0001$. Lower case m represents lower molars; upper case M represents upper molars.

Model	Wilks' lambda	Chi-square	d.f.	Bootstrap (%)	Jackknife (%)
m1	0.590	112.801	8	61.9	60.6
m1-m2	0.473	74.557	16	78.3	65.1
m1-m2-m3	0.089	80.899	24	92.5	78.6
m1-m3	0.234	58.877	16	80.9	66
m2	0.664	72.625	8	67.6	67.6
m2-m3	0.438	58.142	16	83.1	72.7
m3	0.623	39.978	8	82	79.8
mU	0.670	158.568	8	64.3	63.5
M1	0.700	105.994	8	62.3	60.6
M1-M2	0.610	74.371	16	70.7	65.6
M1-M2-M3	0.290	81.073	24	86.5	74.3
M1-M3	0.468	59.548	16	77.6	69.4
M2	0.684	86.419	8	71.1	69.4
M2-M3	0.419	93.412	16	83.3	78.1
M3	0.580	71.564	8	76.5	70.6
MU	0.729	209.902	8	63.9	63.6

Overall, the majority of specimens from grazing species were correctly classified across all models (Fig. 5), but only 35% of species were correctly classified on the basis of median classification score. Of the 20 grazing species examined, two were consistently classified as grazing across all cases (Table 4, Fig. 3E). However, each of these species was represented by a single specimen (= 2 cases). In six additional species, ≥50% of the models produced a grazing classification across all the cases, although the median score for *Kobus leche* was that of a mixed feeder. Five species had models giving less than 50% but greater than 0% grazing classifications. Of these five, four had median mixed-feeder scores, the exception being *Redunca arundinum*, which had a median classification as a browser. Six species had zero classifications in the grazing category.

Lower molars

All eight lower molar LDA models produced statistically significant ($P < 0.0001$) Wilks' lambda values (Table 1). Bootstrap and jackknifed classification values were all better than would be expected if each specimen had an equal chance of being assigned to one of the three dietary categories (i.e. 33%; Table 1). The worst-performing model was the first lower molar, with a jackknifed correct classification rate of 60.6%. The best performing model was the lower third molar, with a jackknifed correct classification rate of 79.8%.

The majority of browsing specimens were correctly classified across all models (Fig. 2) with 80% of species correctly classified on the basis of median classification score. As was the case for the upper molars, of 15 browsing species examined, seven were consistently classified as browsers across all cases examined (Table 5; Fig. 3B). *Cephalophus nigrifrons* was classified as a browser in 79 of the 80 cases run here. Three browsing species misclassified in more than 50 of the analyses. *Tragelaphus buxtoni* and *Tragelaphus euryceros* specimens were frequently misclassified as mixed, while *Cephalophus silvicultor* specimens were frequently misclassified as a grazer across the models (Table 5). The remainder of species were largely classified as browsers.

The majority of specimens from mixed-feeding bovids were correctly classified across all cases (Fig. 4); however, only 36% of species samples were correctly classified on the basis of median score. Only one mixed-feeding species, *Tragelaphus imberbis,* was always classified as a mixed feeder (Table 6; Fig. 3D). However, this is based on only one tooth (m1) and two models (m1 and mU). Specimens from two other species, *Taurotragus oryx*, and *Tragelaphus angasi* were correctly classified in more than 50% of their models. *Antidorcas marsupialis* and *Gazella soemmerringi* were correctly classified in exactly half the models. In two species, *Gazella rufifrons* and *Tragelaphus strepsiceros*, fewer than 50% of cases produce a mixed classification, although the latter still produced a mixed classification. Finally, models for four of the species examined produced no mixed diet classifications. Three of these were consistently classified as browsers.

For grazing species, the majority of specimens examined

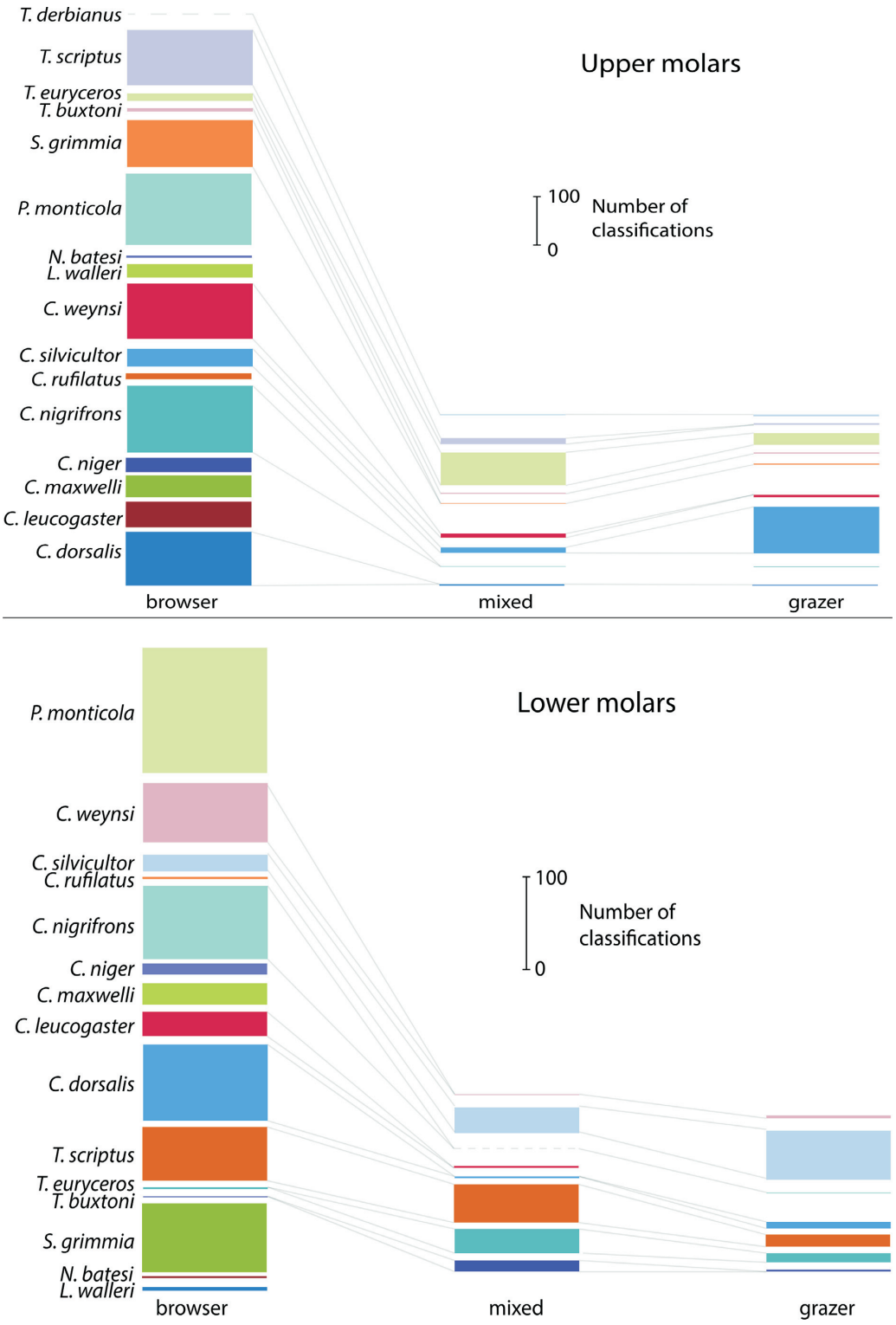


Figure 2. Classifications of each browsing specimen examined for upper (top) and lower (bottom) molars. Dashed lines indicates no specimens within that trophic classification.

were correctly classified across all models (Fig. 5), with 56% of species correctly classified on the basis of median classification score. Sixteen grazing species were examined, with five of these producing consistent grazing classifications across all specimens and models (Table 7; Fig. 3F). In four additional species (*Redunca arundinum, R. redunca, Hippotragus equinus, Kobus ellipsiprymnus*) more than 50% of cases were classified as grazing, while two more species, *Alcelaphus lichtensteini* and *Alcelaphus buselaphus*, had grazing classifications for exactly 50% of cases. Two species, *Gazella thomsoni* and *Tragelaphus spekii*, had fewer than 50% with correct classifications. Finally, three species were always misclassified. For two of these (*Redunca fulvorufula* and *Gazella granti* this was based on only one tooth (m1) and two of the more unsuccessful models (m1 and mU). *Ourebia ourebi* consistently produced an erroneous classification of browser.

Evolutionary history

Dietary classifications are not consistently related to the

Table 2. Classification of browsing species across all upper molar specimens and models: browsers (1); mixed feeders (2); grazers (3).

Species	*n* (specimens)	*n* (models)	Total *n* cases	*n* (classifications) browsing	*n* (classifications) mixed	*n* (classifications) grazing	% Browser	Median classification
Cephalophus dorsalis	22	8	114	109	3	2	95.61404	1
Cephalophus leucogaster	11	8	52	52	0	0	100	1
Cephalophus maxwelli	9	8	44	44	0	0	100	1
Cephalophus niger	6	8	29	29	0	0	100	1
Cephalophus nigrifrons	26	8	137	135	1	1	98.54015	1
Cephalophus rufilatus	2	8	12	12	0	0	100	1
Cephalophus silvicultor	23	8	141	36	11	94	25.53191	3
Cephalophus weynsi	26	8	125	112	8	5	89.6	1
Litocranius walleri	5	8	27	27	0	0	100	1
Neotragus batesi	2	2	4	4	0	0	100	1
Philantomba monticola	17	8	144	144	0	0	100	1
Sylvicapra grimmia	26	8	98	95	1	2	96.93878	1
Taurotragus derbianus	1	4	5	0	2	3	0	3
Tragelaphus buxtoni	2	8	12	7	2	3	58.33333	1
Tragelaphus eurycerus	17	8	106	15	67	24	14.15094	2
Tragelaphus scriptus	22	8	127	112	12	3	88.18898	1

species' evolutionary history (Fig. 6). This can be most clearly observed in the Reduncini. All reduncine species examined here are considered grazers (Gagnon & Chew, 2000) but at least one species, *Redunca fulvorufula*, has a median classification of browser using either upper or lower molars, and four other species (making a total of five out of six Reduncinae) are not classified as grazers using upper molars. Similarly, this trend can be observed in the Cephalophini where at least one species is incorrectly classified according to median score across all possible cases for both upper and lower gnathic rows.

Dietary classification

Both carbon isotope values and mesowear reconstructions made from lower molars were available for 76 specimens (Table 8). Seventy-four per cent ($n = 56$) of the specimens had their diets, as determined by $\delta^{13}C$ values, correctly identified by the median LDA classification across all models. It should be noted that the majority of these specimens were browsers. Twenty specimens (26%) had median reconstructions suggesting a diet different from that suggested by the $\delta^{13}C$ values. Incorrect classifications are not solely based on inaccurate determination of diet from the literature. Specimen 12608, *Tragelaphus eurycerus*, had one of the lowest $\delta^{13}C$ values recorded, entirely consistent with its classification as a browser by Gagnon & Chew (2000). However, the reconstructions made of the basis of its molar morphology assigned it as either a mixed feeder (five of the nine models) or grazer (four of the nine models). Specimen 16849, *Redunca redunca*, a species considered an obligate grazer by Gagnon & Chew (2000), had a high $\delta^{13}C$ value consistent with this dietary classification. Nevertheless, four of the five mesowear models predicted that this specimen was a browser.

For specimens where both carbon isotope values and mesowear reconstructions from upper molars were available, 76% ($n = 65$) had their diets, as determined by $\delta^{13}C$ values, correctly identified by the median LDA classification across all models. As was the case for lowers molars, incorrect classifications were not solely based on inaccurate categorization. Examples for upper molars include four specimens of *Redunca redunca*, who according to their dietary classification and $\delta^{13}C$ values are grazers; however, the mesowear models reconstruct them as either browsers or mixed feeders. Likewise the *Cephalophus silvicultor* specimens, which are browsers according to the diet classification scheme and isotopic record, were classified according to the models as grazers.

Body size

Comparisons between proportions of correctly classified specimens within browsers and body mass produced a significant relationship (upper molars: $r_s = -0.7907$, $P < 0.001$; lower molars $r_s = -0.66594$, $P = 0.013$). Likewise grazers produced an equally significant, though directly inverse relationship (upper molars: $r_s = 0.73128$, $P < 0.001$; lower molars $r_s = 0.0.55123$, $P = 0.033$). The proportion of correctly classified mixed feeders was not significantly correlated with body mass for upper molars ($r_s = 0.56237$, $P = 0.057$), although this approaches statistical significance, and was not replicated for lower molars ($r_s = 0.86275$, $P < 0.001$). The positive r_s value obtained for mixed feeders is similar to that of grazers, indicating that like grazers, large-bodied mixed feeders tend to be correctly classified, while small-bodied mixed feeders tend to be misclassified in our models. Such correlations help explain the poor success our models had in classifying larger browsers like *C. silvicultur*, *T. derbianus*, and *T. eurycerus*, and smaller grazers like *R. fulvorufula*, *G. granti*, *O. ourebi*.

The strong influence of body size on our analyses is observable in the relative absolute size of the coefficients of each of the metric variables in individual LDAs. Calculated as a percentage of overall coefficient values for each LDA, tooth length and tooth breadth had on average the highest values for discriminant functions 1 and 2, across both upper and lower molar models (Table 9). The only exception was for discriminant function 1, where

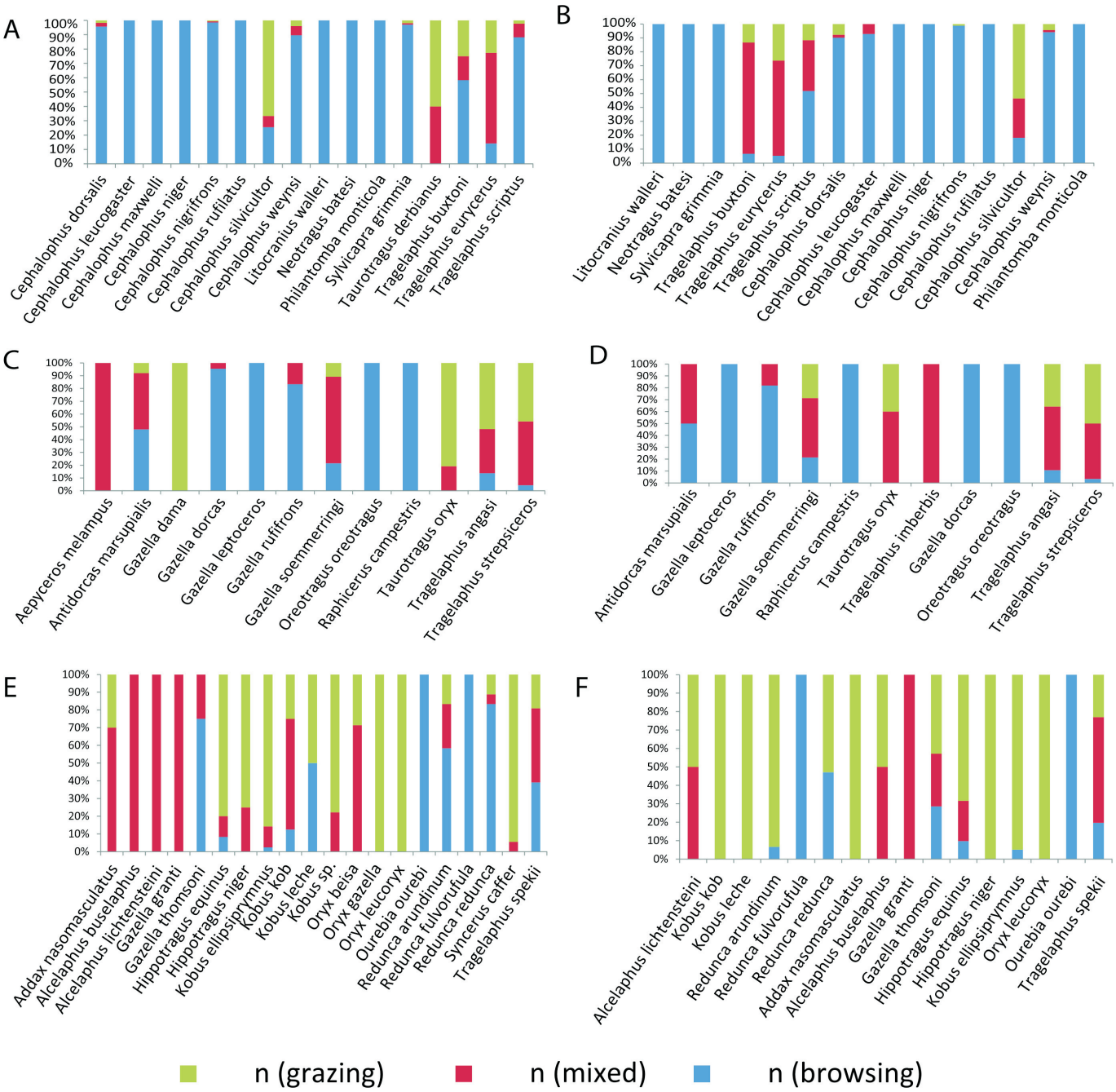


Figure 3. Classification of each browsing bovid species examined. Green represents a grazing classification, red mixed, and blue browsing. **A,** browsers, upper molars; **B,** browsers, lower molars; **C,** mixed feeders, upper molars; **D,** mixed feeders, lower molars; **E,** grazers, upper molars; **F,** grazers, lower molars.

in the upper tooth models crown height had on average a relatively higher coefficient value than tooth breadth (but not height). This indicates that across almost all the models the variables more closely correlated with body size (tooth length and breadth) than with degree of wear (crown height and occlusal relief height) are influencing dietary reconstructions. Considering the usually higher relative coefficient values for tooth length and breadth across the models it is not surprising that subsequent classification scores are strongly correlated to body size.

This strong correlation prompted us to re-examine what effects removing body size would have on our models. We therefore implemented a number of commonly employed techniques for adjusting raw values for body size (see Louys *et al.* 2013; Meloro *et al.* 2013). These included (1) log transformation of all variables, where the raw variables were first transformed by adding 1 (in order to allow inclusion of specimens with occlusal height of 0); (2) a principal components analysis of raw variables, whereby the first principal component is significantly and strongly correlated with body size, and is thus removed; (3) ratios calculated from raw variables; and (4) residuals, in our case produced from a multivariate regression between the length of the anteriormost molar (itself strongly and significantly correlated with body size, *cf.* Damuth & MacFadden 1990; Janis 1990) and all other variables in each respective model. In light of the similarity between classification accuracy and body size for mixed feeders and grazers, these trophic groups were combined for the

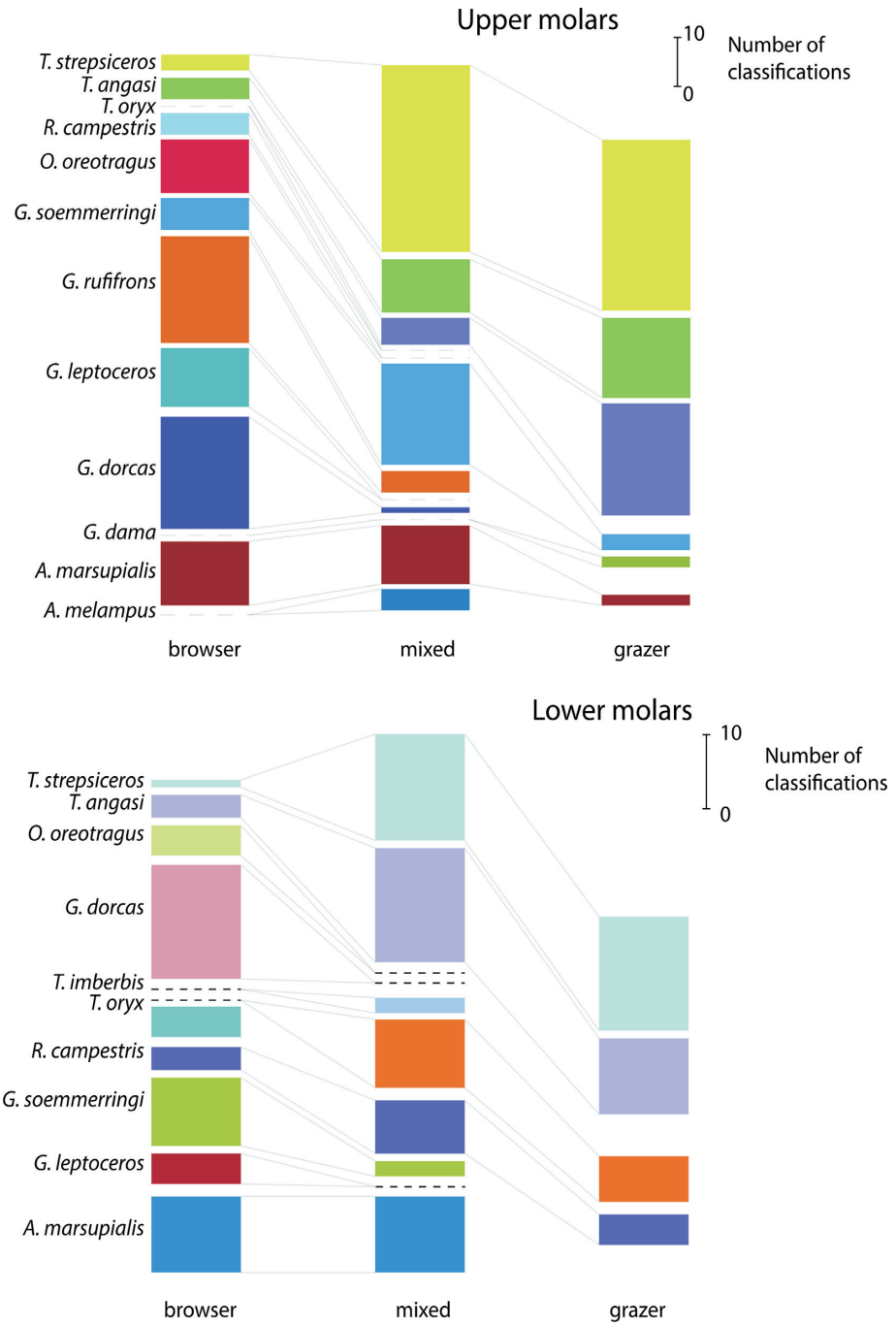


Figure 4. Classifications of each mixed-feeding specimen examined for upper (top) and lower (bottom) molars. Dashed lines indicates no specimens within that trophic classification.

Table 3. Classification of mixed-feeder species across all upper molar specimens and models: browsers (1); mixed feeders (2); grazers (3).

Species	*n* (specimens)	*n* (models)	Total *n* cases	*n* (classifications) browsing	*n* (classifications) mixed	*n* (classifications) grazing	% Browser	Median classification
Aepyceros melampus	2	2	4	0	4	0	100	2
Antidorcas marsupialis	7	8	25	12	11	2	44	2
Gazella dama	1	2	2	0	0	2	0	3
Gazella dorcas	11	2	22	21	1	0	4.545455	1
Gazella leptoceros	4	4	11	11	0	0	0	1
Gazella rufifrons	9	4	24	20	4	0	16.66667	1
Gazella soemmerringi	7	8	28	6	19	3	67.85714	2
Oreotragus oreotragus	1	8	10	10	0	0	0	1
Raphicerus campestris	2	2	4	4	0	0	0	1
Taurotragus oryx	6	8	26	0	5	21	19.23077	3
Tragelaphus angasi	5	8	29	4	10	15	34.48276	3
Tragelaphus strepsiceros	10	8	70	3	35	32	50	2

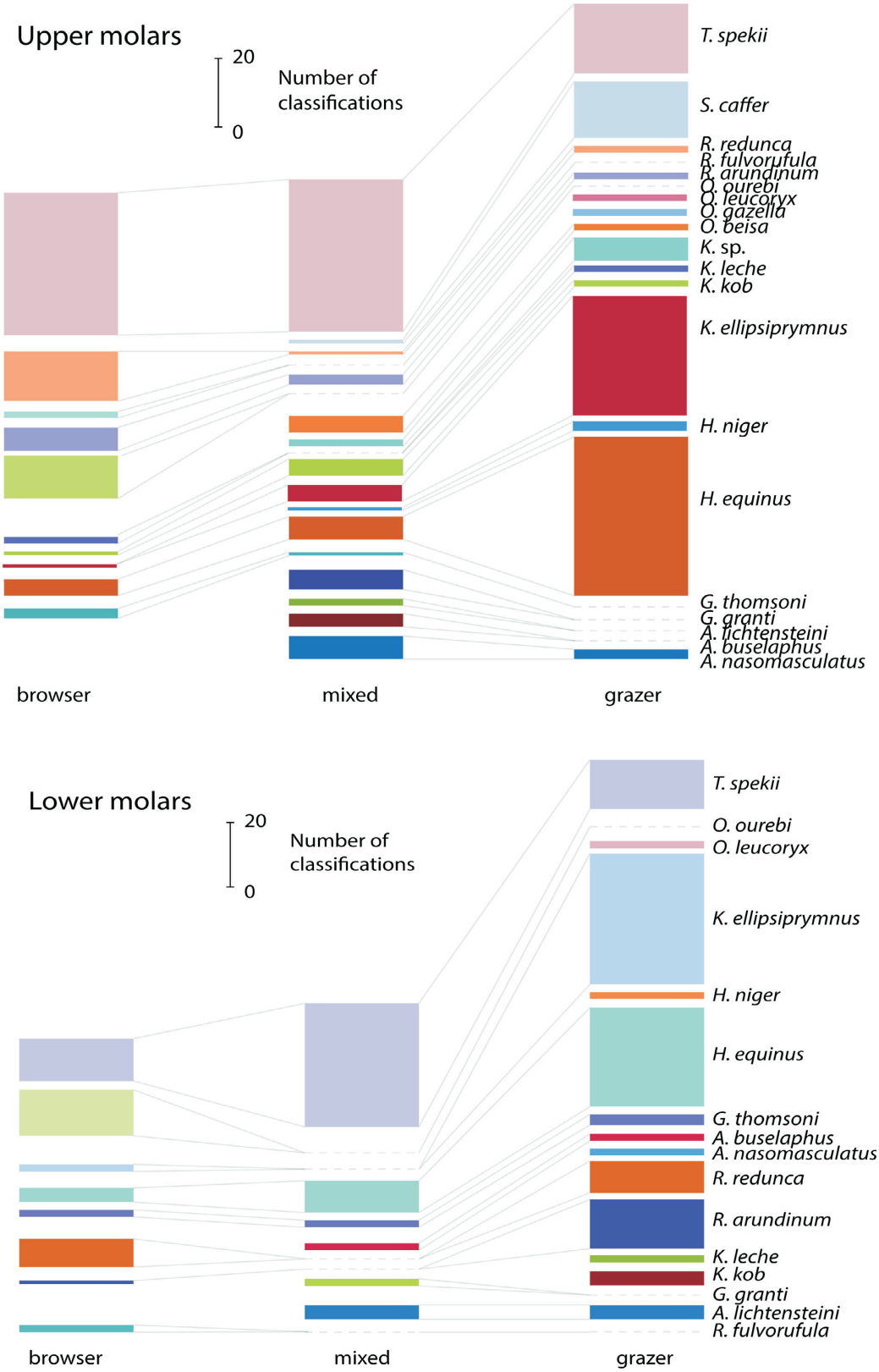


Figure 5. Classifications of each grazing specimen examined for upper (top) and lower (bottom) molars. Dashed lines indicates no specimens within that trophic classification.

purposes of these comparisons. The effect of removing body size for each model was determined by examining the *F*-values of the ensuing LDA, a measure of between-groups relative to within-groups separation. All body size-corrected models showed consistently poorer discriminant results compared to raw values with only one exception, the lower second molar (Table 10).

DISCUSSION

A summary of the classification results is presented in Table 11. Overall, each model worked relatively well, with classification accuracies of between ~60–80% depending on the model. In addition, the majority of specimens within each dietary category provided correct dietary classifications (Figs 2 and 5). The only exception was that

Table 4. Classification of grazing species across all upper molar specimens and models: browsers (1); mixed feeders (2); grazers (3).

Species	*n* (specimens)	*n* (models)	Total *n* cases	*n* (classifications) browsing	*n* (classifications) mixed	*n* (classifications) grazing	% Grazer	Median classification
Addax nasomasculatus	1	8	10	0	7	3	30	2
Alcelaphus buselaphus	2	2	4	0	4	0	0	2
Alcelaphus lichtensteini	1	2	2	0	2	0	0	2
Gazella granti	3	2	6	0	6	0	0	2
Gazella thomsoni	2	2	4	3	1	0	0	1
Hippotragus equinus	20	8	60	5	7	48	80	3
Hippotragus niger	2	2	4	0	1	3	75	3
Kobus ellipsiprymnus	15	4	42	1	5	36	85.71429	3
Kobus kob	4	2	8	1	5	2	25	2
Kobus leche	2	2	4	2	0	2	50	2
Kobus sp.	3	4	9	0	2	7	77.77778	3
Oryx beisa	2	4	7	0	5	2	28.57143	2
Oryx gazella	1	2	2	0	0	2	100	3
Oryx leucoryx	1	2	2	0	0	2	100	3
Ourebia ourebi	5	4	13	13	0	0	0	1
Redunca arundinum	6	2	12	7	3	2	16.66667	1
Redunca fulvorufula	1	2	2	2	0	0	0	1
Redunca redunca	9	2	18	15	1	2	11.11111	1
Syncerus caffer	6	4	18	0	1	17	94.44444	3
Tragelaphus spekii	20	8	110	43	46	21	19.09091	2

Table 5. Classification of browsing species across all lower molar specimens and models: browsers (1); mixed feeders (2); grazers (3).

Species	*n* (specimens)	*n* (models)	Total *n* cases	*n* (classifications) browsing	*n* (classifications) mixed	*n* (classifications) grazing	% Browser	Median classification
Litocranius walleri	1	4	4	4	0	0	100	1
Neotragus batesi	1	2	2	2	0	0	100	1
Sylvicapra grimmia	23	8	74	74	0	0	100	1
Tragelaphus buxtoni	3	8	15	1	12	2	6.666667	2
Tragelaphus eurycerus	9	8	38	2	26	10	5.263158	2
Tragelaphus scriptus	22	8	112	58	41	13	51.78571	1
Cephalophus dorsalis	18	8	91	82	2	7	90.10989	1
Cephalophus leucogaster	10	4	28	26	2	0	92.85714	1
Cephalophus maxwelli	9	4	23	23	0	0	100	1
Cephalophus niger	5	4	12	12	0	0	100	1
Cephalophus nigrifrons	21	8	80	79	0	1	98.75	1
Cephalophus rufilatus	1	2	2	2	0	0	100	1
Cephalophus silvicultor	22	8	99	18	28	53	18.18182	2.5
Cephalophus weynsi	21	8	68	64	1	3	94.11765	1
Philantomba monticola	17	8	135	135	0	0	100	1

Table 6. Classification of mixed-feeding species across all lower molar specimens and models: browsers (1); mixed feeders (2); grazers (3).

Species	*n* (specimens)	*n* (models)	Total *n* cases	*n* (classifications) browsing	*n* (classifications) mixed	*n* (classifications) grazing	% Mixed	Median classification
Antidorcas marsupialis	7	4	20	10	10	0	50	1.5
Gazella leptoceros	2	2	4	4	0	0	0	1
Gazella rufifrons	4	4	11	9	2	0	18.18182	1
Gazella soemmerringi	6	4	14	3	7	4	50	2
Raphicerus campestris	2	2	4	4	0	0	0	1
Taurotragus oryx	3	8	15	0	9	6	60	2
Tragelaphus imberbis	1	2	2	0	2	0	100	2
Gazella dorcas	6	4	15	15	0	0	0	1
Oreotragus oreotragus	1	4	4	4	0	0	0	1
Tragelaphus angasi	4	8	28	3	15	10	53.57143	2.5
Tragelaphus strepsiceros	7	8	30	1	14	15	46.66667	2

Table 7. Classification of grazing species across all lower molar specimens and models: browsers (1); mixed feeders (2); grazers (3).

Species	*n* (specimens)	*n* (models)	Total *n* cases	*n* (classifications) browsing	*n* (classifications) mixed	*n* (classifications) grazing	% Grazer	Median classification
Alcelaphus lichtensteini	4	2	8	0	4	4	50	2.5
Kobus kob	2	2	4	0	0	4	100	3
Kobus leche	1	2	2	0	0	2	100	3
Redunca arundinum	6	4	15	1	0	14	93.33333	3
Redunca fulvorufula	1	2	2	2	0	0	0	1
Redunca redunca	7	4	17	8	0	9	52.94118	3
Addax nasomasculatus	1	2	2	0	0	2	100	3
Alcelaphus buselaphus	2	2	4	0	2	2	50	2.5
Gazella granti	1	2	2	0	2	0	0	2
Gazella thomsoni	2	4	7	2	2	3	42.85714	2
Hippotragus equinus	11	8	41	4	9	28	68.29268	3
Hippotragus niger	1	2	2	0	0	2	100	3
Kobus ellipsiprymnus	14	4	39	2	0	37	94.87179	3
Oryx leucoryx	1	2	2	0	0	2	100	3
Ourebia ourebi	5	4	13	13	0	0	0	1
Tragelaphus spekii	14	8	61	12	35	14	22.95082	2

of mixed-diet upper molar specimens, where the majority of specimens were misclassified as browsers (Fig. 4). This was not entirely surprising: we might expect that mixed feeders would display the worst classification scores as they encompass such wide-ranging diets, and even in this instance a large proportion of specimens were still correctly classified as mixed feeders. The absence of 'mixed feeders' amongst all modern African herbivores in carbon isotope analysis (Cerling *et al.* 1999), as well as in fossil ungulates from southern Africa (Codron *et al.* 2008), suggests that this trophic category may merely reflect the end points of grazing dominated or browse dominated dietary spectrums (Louys and Faith, in press), and further explaining the poor performance of this diet classification when compared to either the grazing or browsing groups.

The evolutionary history of a species will undoubtedly have an influence on its dietary preferences, such that some level of niche conservatism is to be expected within a closely related group of organisms. However, if niche conservatism was entirely controlling dietary classifications, we would expect diets of closely related species to be the dominant dietary category for all species within a clade. Our results illustrated on Fig. 6 suggest otherwise. While some niche conservatism was expected, our results suggest that the models developed here can in most instances accurately detect different diets even between closely related species using LDAs. However, a strong caveat is that the models failed to accurately predict diet when specimen classifications were averaged within species for mixed and grazing species.

Body size overwhelmingly influenced dietary classifications in our models, with smaller-bodied species tending to browsing classifications and larger-bodied species tending to more grazing related diets. A number of researchers have previously shown that diet is significantly correlated, albeit weakly, with body size (Gagnon & Chew, 2000; Perez-Barberia & Gordon 2001; Louys & Faith, in press). The models we developed obviously exploit this correlation. Given the previously observed weakness of correlation between body size and diet, however, it was surprising that body size had such a strong influence on our models. Body size was so influential that when its effects were removed, discrimination between the broadly defined trophic groups was greatly, and in many instances significantly, reduced. The strong correlation between classification scores and body size was driven by the much larger influence that tooth length and breadth had on the majority of our models than either variable directly associated with tooth wear (i.e. crown height or occlusal relief height). Both crown height and occlusal relief height will, to a large extent, be a function of an individual's age. Although we collected measurements from only prime adults – excluding old and juvenile specimens – nevertheless absolute values for these variables, and in particular crown height, can vary considerably between the younger and more mature individuals of the adults examined. The lowest relative influence of crown height in a single tooth position was in the upper third molar (Table 9). In even this model, however, where the LDA coefficient for crown height represents only 2.6% of the total coefficient values for discriminant function 1 (itself accounting for 98.8% of the variance of the data), crown height between trophic groups is significantly different ($P < 0.01$, d.f. = 2, 133, $F = 14.94$), indicating that age-related crown height differences within trophic groups were minimal compared to between trophic groups. Thus the relatively smaller influence of crown height in most of our models compared to tooth length and breadth – more so than might be expected given the importance of this variable for hypsodonty index calculations – was not due to age-related crown height differences amongst adults. Crown height and occlusal relief height, while on average having a smaller influence on the LDAs than tooth length or breadth, nevertheless are significant for many of the models developed here. The distribution of high coefficient values for these tooth wear variables is not intuitively or evenly distributed across the

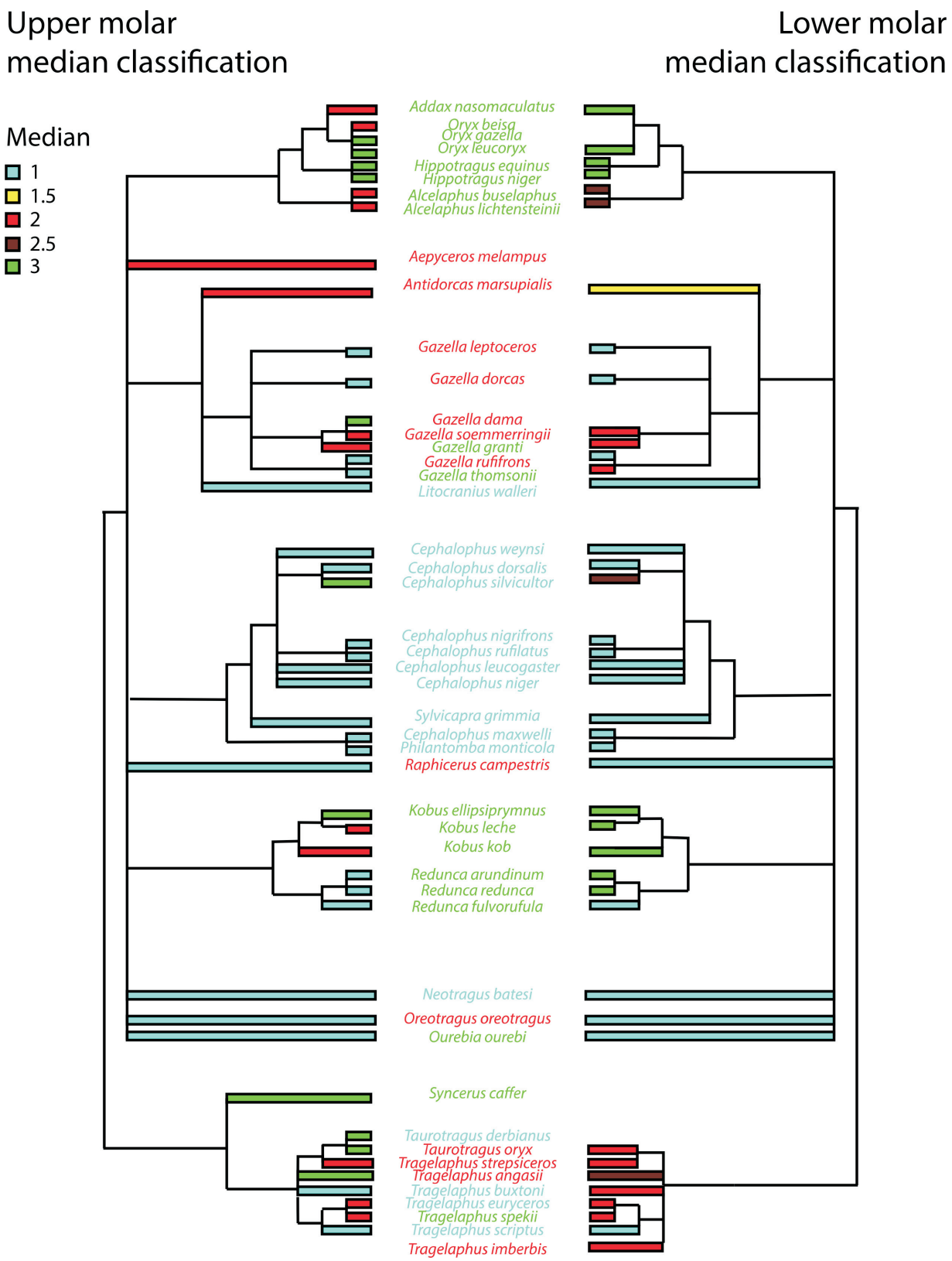


Figure 6. Median classification for each species mapped on the phylogenetic tree of the Bovidae according to Price (2005). Green represents a grazing classification, red mixed, and blue browsing. Left-hand side represents the upper molars, right-hand side the lower molars.

models, arguing against their *ad hoc* removal in future analyses.

While body size differences clearly contributed to classification accuracies, nevertheless only species belonging to the browsing category had consistently high classification rates on the basis of median scores. While individual specimens are relatively well classified by the models, as indicated by the comparisons with the isotopic record, when classifications were averaged across species, or when individual teeth were examined, only browsers were consistently assigned to their correct dietary category across all models. This result was unexpected, but is likely due to the much lower specimen and model samples available for grazing and mixed-feeding species. This sampling bias

Table 8. List of misclassified specimens with diets assigned according to their $\delta^{13}C$ record. Diet classifications: browsers (1); mixed feeders (2); grazers (3).

Specimen number (RMCA)	Species	Diet category (reduced Gagnon & Chew)	$\delta^{13}C$ (Louys *et al.* 2012)	$\delta^{13}C$ diet classification	Median classification (upper molars)	Median classification (lower molars)
2222	*Cephalophus silvicultor*	Browser	–25.62	1	3	3
10217	*Cephalophus silvicultor*	Browser	–24.03	1	n/a	3
10429	*Cephalophus silvicultor*	Browser	–24.16	1	3	n/a
15636	*Cephalophus silvicultor*	Browser	–23.67	1	n/a	3
15700	*Cephalophus silvicultor*	Browser	–24.09	1	n/a	1.5
18514	*Cephalophus silvicultor*	Browser	–23.53	1	3	n/a
27769	*Cephalophus silvicultor*	Browser	–24.1	1	2.5	2
5302	*Cephalophus weynsi*	Browser	–17.8128	2	1	1
22264	*Hippotragus equinus*	Variable grazer	–16.2927	2	3	3
28661	*Redunca arundinum*	Obligate grazer	–9.6498	3	1	n/a
1180	*Redunca redunca*	Obligate grazer	–8.39803	3	1	1
2351	*Redunca redunca*	Obligate grazer	–8.51913	3	2	n/a
5495	*Redunca redunca*	Obligate grazer	–7.60845	3	1	n/a
5497	*Redunca redunca*	Obligate grazer	–7.83607	3	1	n/a
16849	*Redunca redunca*	Obligate grazer	–8.31553	3	n/a	1
1224	*Sylvicapra grimmia*	Browser	–21.3611	2	1	1
19212	*Sylvicapra grimmia*	Browser	–21.8308	2	1	1
26899	*Sylvicapra grimmia*	Browser	–23.1719	1	1.5	n/a
12608	*Tragelaphus eurycerus*	Browser	–30.1086	1	2	n/a
12608	*Tragelaphus eurycerus*	Browser	–30.1086	1	n/a	2
1255	*Tragelaphus scriptus*	Browser	–23.5289	1	2	n/a
3884	*Tragelaphus scriptus*	Browser	–23.7254	1	n/a	1.5
5522	*Tragelaphus scriptus*	Browser	–23.3332	1	n/a	2
14638	*Tragelaphus scriptus*	Browser	–23.1427	1	n/a	2
37466	*Tragelaphus scriptus*	Browser	–23.3871	1	n/a	1.5
171	*Tragelaphus spekii*	Variable grazer	–26.117	1	2	2
336	*Tragelaphus spekii*	Variable grazer	–23.4343	1	n/a	2
337	*Tragelaphus spekii*	Variable grazer	–23.4343	1	2	n/a
7932	*Tragelaphus spekii*	Variable grazer	–18.7278	2	2.5	2
14619	*Tragelaphus spekii*	Variable grazer	–25.62	1	2.5	3
28663	*Tragelaphus spekii*	Variable grazer	–24.5131	1	2	n/a

was primarily due to the availability of pristine molars in the larger-sized bovids we examined. Additionally, the number of specimens where the tooth crown height was preserved above the level of the mandible or maxilla was fewer in larger-bodied species than in smaller species, further lowering the number of measurements possible for larger-bodied individuals. This bias impacted on the number of whole tooth rows measured for grazing and mixed feeders, with often only one tooth in a gnathic row yielding teeth suitable for measurement. The net effect of this body-size bias was a lower total number of models that could be applied for each grazing and mixed feeding bovid, and a reduction in the number of larger bodied species in our analyses.

The large number of correct classifications for browsing species in conjunction with the much higher specimen and model numbers led to the overall high classification rates observed. Hence, although there are sufficient specimen numbers across the three dietary categories to confidently separate them in multivariate space (Table 1), the limited specimen numbers per species within the mixed-feeder and grazer trophic groups means species' diets cannot at present be distinguished confidently on the basis of most of the models developed here (although some do provide high levels of classifications). The possibility remains that the lack of phylogenetic signal observed in our analyses may be the direct result of the incorrect median classifications obtained for mixed feeders and grazers. The addition of more small-bodied grazing and large-bodied browsing specimens may significantly increase the proportion of correct classifications.

Higher classifications may also be achieved by adding more variables (e.g. measurements) in the models. For example, the use of Elliptical Fourier Function analysis of the occlusal surface of teeth has provided more accurate dietary classifications for twenty closely related bovid taxa than we were generally able to achieve in our models (Brophy *et al.* 2014). However, such analyses considerably add to data collection and processing time, negating one of the huge advantages of methods such as mesowear analysis and the approach we tested here. Our measurements were chosen as they are simple and quick to take, and are informative of some aspect of the animal's ecology: molar length is closely correlated with body size (Damuth & MacFadden 1990; Janis 1990), in turn associated with bovid dietary preferences (Gagnon & Chew 2000; Pérez-Barbería & Gordon 2001). Crown height in conjunction with molar breadth provides an indication of the hypsodonty index of a species, in turn highly correlated with diet (Janis 1995; Mendoza & Palmqvist 2007; Raia *et al.* 2010). That high classification rates were achieved consistently for browsers suggests the use of minimal variables holds promise for accurate dietary predictions provided sample sizes across taxa, body size, and trophic groups are sufficient, although some easily acquired, size-free variables (e.g. cusp sharpness) may need to be

Table 9. Absolute size of the coefficients of each of the metric variables included in the individual linear discriminant analyses (LDA), presented as a percentage of the total of the coefficient values for each LDA (listed to two decimal places). Figures in bold indicate the variance explained by the two discriminant functions for each model. ORH: occlusal relief height; ORL: tooth length; HIH: crown height; HIB: tooth breadth.

Model	Function 1	Function 2	Model	Function 1	Function 2
lower m1	**91.50**	**8.50**	**upper M1**	**96.30**	**3.70**
Lm1-HIB	36.42	28.03	LM1-HIH	59.90	6.25
Lm1-ORL	35.48	50.59	LM1-HIB	23.50	34.55
Lm1-HIH	27.76	18.30	LM1-ORH	16.43	13.05
Lm1-ORH	0.34	3.08	LM1-ORL	0.17	46.15
lower m1-m2	**68.50**	**31.50**	**upper M1-M2**	**76.10**	**23.90**
Lm1-HIB	35.76	33.96	LM1-HIB	24.76	2.02
Lm2-HIB	24.40	28.41	LM2-HIH	19.58	16.47
Lm1-ORL	14.75	0.73	LM1-HIH	16.01	4.60
Lm2-ORH	10.85	4.63	LM2-HIB	15.54	25.02
Lm1-ORH	6.85	2.70	LM1-ORL	7.32	0.51
Lm2-HIH	4.65	6.42	LM2-ORL	6.19	41.98
Lm2-ORL	2.18	22.06	LM2-ORH	5.58	1.18
Lm1-HIH	0.55	1.08	LM1-ORH	5.03	8.24
lower m1-m2-m3	**85.20**	**14.80**	**upper M1-M2-M3**	**77.40**	**22.60**
Lm2-ORL	22.83	19.97	LM3-ORL	26.74	4.66
Lm1-HIB	18.10	1.10	LM2-ORL	26.57	7.07
Lm3-HIB	12.02	3.71	LM2-HIB	10.45	1.80
Lm2-HIB	11.22	21.04	LM1-HIB	10.17	20.85
Lm3-ORL	8.35	2.75	LM1-ORL	6.49	11.73
Lm1-ORL	7.44	5.35	LM3-HIH	4.50	0.72
Lm1-HIH	5.96	6.23	LM3-ORH	4.20	3.08
Lm2-HIH	4.24	13.24	LM1-HIH	2.90	10.59
Lm2-ORH	3.53	7.94	LM2-ORH	2.61	1.78
Lm3-HIH	2.65	6.67	LM2-HIH	2.41	17.85
Lm3-ORH	2.27	4.65	LM1-ORH	2.27	2.12
Lm1-ORH	1.39	7.37	LM3-HIB	0.68	17.75
lower m1-m3	**92.00**	**8.00**	**upper M1-M3**	**86.30**	**13.70**
Lm3-ORL	39.71	34.93	LM3-ORL	37.96	9.70
Lm1-ORL	20.79	22.70	LM1-ORL	17.19	15.77
Lm1-HIB	12.89	15.71	LM3-ORH	11.83	3.42
Lm3-ORH	9.49	5.48	LM3-HIH	11.80	9.43
Lm1-HIH	4.90	1.82	LM1-HIB	8.66	29.52
Lm3-HIH	4.59	16.89	LM1-ORH	6.31	3.32
Lm3-HIB	4.39	0.01	LM3-HIB	3.15	25.25
Lm1-ORH	3.24	2.45	LM1-HIH	3.10	3.59
lower m2	**78.60**	**21.40**	**upper M2**	**78.20**	**21.80**
Lm2-HIB	32.47	22.31	LM2-HIH	34.83	17.02
Lm2-ORL	27.79	50.09	LM2-ORL	32.31	46.83
Lm2-ORH	22.65	5.02	LM2-HIB	30.41	29.39
Lm2-HIH	17.09	22.58	LM2-ORH	2.44	6.76
lower M2-m3	**68.40**	**31.60**	**upper M2-M3**	**93.70**	**6.30**
Lm3-ORL	35.34	15.54	LM3-ORL	41.18	7.55
Lm3-HIH	14.76	10.67	LM2-ORL	28.73	32.21
Lm2-HIH	13.75	4.28	LM3-HIH	9.09	11.08
Lm 2-HIB	13.12	18.27	LM3-ORH	7.72	4.26
Lm2-ORH	7.92	11.40	LM2-HIB	6.84	10.90
Lm3-HIB	7.03	17.63	LM2-ORH	2.90	14.79
Lm2-ORL	5.96	13.00	LM3-HIB	2.33	14.17
Lm3-ORH	2.13	9.20	LM2-HIH	1.22	5.03
lower m3	**82.80**	**17.20**	**upper M3**	**98.80**	**1.20**
Lm3-ORL	54.63	45.16	LM3-ORL	54.52	42.56
Lm3-HIB	35.85	23.05	LM3-ORH	28.03	0.23
Lm3-ORH	6.45	7.75	LM3-HIB	14.84	34.55
Lm3-HIH	3.07	24.04	LM3-HIH	2.61	22.66
lower mu	**85.40**	**14.60**	**upper MU**	**87.30**	**12.70**
LmU-ORL	36.10	52.24	LMU-HIH	34.87	13.66
LmU-HIB	34.28	24.97	LMU-ORH	26.91	10.17
LmU-HIH	24.48	21.48	LMU-HIB	21.05	28.42
LmU-ORH	5.14	1.31	LMU-ORL	17.17	47.75
MEAN					
ORL	23.95	25.78	ORL	23.27	24.19
ORH	6.33	5.61	ORH	9.40	5.57
HIH	9.88	11.82	HIH	15.60	10.69
HIB	21.38	18.32	HIB	13.26	21.09

Table 10. *F*-values of LDAs constructed from size-corrected variables. PCs refers to principal components analysis with the first principal component omitted.

Model	upper M1	upper M1-M2	upper M1-M2-M3	upper M1-M3	upper M2	upper M2-M3	upper M3	upper MU
Raw	23.483	8.093	6.8581	7.8433	18.728	15.41	22.399	46.943
Logged	22.144	6.8347	5.1088	5.7769	17.744	10.685	18.625	40.667
PCs	2.5475	1.2367	3.0261	3.233	0.05899	6.2527	6.8668	5.6846
Ratios	16.07	4.4113	0.87826	1.1718	5.2417	0.54619	1.0217	9.7717
Multivariate residual	4.6006	1.5278	3.294	4.4629	0.19681	7.4115	5.6389	8.8777
	lower m1	lower m1-m2	lower m1-m2-m3	lower m1-m3	lower M2	lower M2-m3	lower m3	lower mU
Raw	19.145	5.8268	7.1826	4.6382	14.659	5.4796	9.2396	26.589
Logged	17.089	5.1986	3.3753	3.8864	15.158	4.4072	7.9835	23.854
PCs	1.2864	0.84078	1.7643	0.72838	1.5709	2.1646	1.9138	1.9299
Ratios	5.263	2.0516	0.44795	1.9433	3.2648	1.1291	1.8124	5.4987
Multivariate residual	3.6925	1.2532	2.2662	1.4072	2.3472	2.277	1.859	4.927

Table 11. Summary of model performances. Classification of specimens based on jackknife analyses, classification of species based on median classification across models.

Model	*n*	Correctly classified specimens (%)				Correctly classified species (%)			
		Browse	Mixed	Graze	Total	Browse	Mixed	Graze	Total
Upper M1	302	78	23	54	61	75	8	40	44
Upper M2	232	80	40	46	69	69	8	25	35
Upper M3	136	83	56	7	71	81	16	0	31
Upper M1, M2	157	78	37	27	66	69	8	10	29
Upper M1, M2, M3	75	86	40	38	75	75	16	0	29
Upper M1, M3	85	81	50	22	69	75	16	0	29
Upper M2, M3	114	89	42	38	78	81	16	5	33
Upper MU	668	76	33	46	63	81	16	35	45
Lower m1	217	70	29	42	61	71	20	53	51
Lower m2	179	75	39	50	68	69	25	55	53
Lower m3	88	89	57	60	80	85	40	67	71
Lower m1, m2	105	74	38	53	66	73	33	71	63
Lower m1, m2, m3	42	85	75	25	76	78	67	0	64
Lower m1, m3	47	73	80	0	66	70	67	0	56
Lower m2, m3	76	76	67	25	72	67	60	0	58
Lower mU	397	83	38	58	64	73	36	50	55

M = upper; m = lower; 1 = first molar, 2 = second molar, 3 = third molar; U = unknown.

included in future models in order to achieve higher levels of predictive accuracy.

Given the small number of variables we selected, it was expected that predictive accuracies achieved in our models would not be as high as other currently employed palaeodietary reconstructive methods. However, it was hoped at the beginning of this study that increasing the number of models applied to individual specimens would provide an averaged classification result that would negate any effects of models yielding less accurate jackknife classifications than desirable. So, for example, if a specimen were represented by an entire mandible, the application of increasingly accurate models (in this instance, m1, mU, m1-m2, m1-m3, M2, M2-m3, m1-m2-m3, m3) would drive median classifications closer to the true value. However this scenario was only observed for a small number of specimens. Of the specimens yielding more than one dietary classification across the models, some had their diets accurately reconstructed when the classification results were averaged across all the models, while others produced incorrect median classifications. These results were replicated when species-averaged classifications were calculated.

Despite the limitations outlined in this study, the comparisons between specimen classifications and the carbon isotope record supports the jackknife values obtained for the LDAs, and provides us with some confidence that the majority of specimens can be assigned to correct diet using these models. When applied to fossil assemblages in conjunction with other palaeoecological proxies, the use of the models described here should provide an additional indication of the primary feeding mode of the bovid palaeocommunity, and thus help inform the likely palaeoenvironment present at the time the fossils were deposited.

CONCLUSIONS

The diets of African bovid specimens can be accurately predicted on the basis of some of the LDA models constructed from simple linear measurements of their molars. Overall accuracy of the models ranged from approximately 60% to 80%, although these decreased

significantly when some tooth positions, and mixed feeders and grazers were examined individually. Body size was a highly significant predictor of the inaccurate classifications obtained in our models, with larger bodied species tending to grazing classifications and smaller bodied species browsing classifications. Nevertheless, 72–75% of specimens had their actual diets, as determined from their stable carbon isotope record, accurately predicted by median LDA score for lower and upper molar models respectively. For each dietary category, the dominant classification obtained across all the specimens reflected that category, with the exception of mixed feeders calculated through upper molar models. When upper and lower models were pooled however, this exception did not hold.

The models failed to accurately reconstruct the dominant diets of most grazing and mixed-feeding species examined, and this is most likely related to the more limited sample sizes and model numbers available for larger bodied species. Overall, lower molars performed better than upper molars at the species level. Some species had their diets consistently and accurately classified regardless of model used. Other species had accurately reconstructed diets when the classification results were averaged across all models. Some species had their diets correctly reconstructed in some models, although the average across models produced incorrect classifications. Finally, some species were consistently misclassified regardless of model. Thus when sufficient specimens can be identified to the species level, traditional mesowear analyses should be favoured over the models developed here.

Misclassifications do not appear to be consistent across sister-groups or clades, and the isotopic record indicates that it was not due to individual differences in diet across specimens. Rather it seems it was an artefact of the way the LDAs were constructed, and specifically the specimens used to construct those models. Lower specimen numbers within mixed feeding and grazing, and hence larger-bodied, species probably accounts for most of these patterns. The input of additional specimens into the models, particularly of (larger-bodied) grazers and mixed feeders, might help negate most of these misclassifications. Including a wider sample of species, especially of those outside the Bovidae, may further increase classification rates, as is the case in traditional mesowear analyses (Louys *et al.* 2011).

In any ecomorphological study there is a balance between the amount of morphological detail captured by metric variables and the accuracy of the predictions that come from analysing those variables. Nevertheless, and despite the limitations discussed above, the dietary preferences of the majority of individual specimens were accurately reconstructed, meaning that dietary reconstructions of fossils can LDA score be achieved with some level of confidence (although such reconstructions will need to be tempered by an appreciate of the likely body size of any analysed specimen). The models described here provide an additional, simple tool for inferring the diets of extinct African bovids on the basis of their dentition, that, when used in combination with other palaeoecological proxies, may help unravel the palaeoenvironmental backdrop under which hominins evolved.

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