Geometric morphometric analysis of snout shape in extant ruminants (Ungulata, Artiodactyla)

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Abstract

Snout shape is a prominent aspect of herbivore feeding ecology, controlling both forage selectivity and intake rate. Many previous investigations have suggested that ruminant feeding classes can be discriminated via snout shape, with grazing and browsing species attributed 'blunt' and 'pointed' snouts respectively, with an intermediate sub-grouping. This aspect of functional ecology is analysed for the first time using a statistically rigorous geometry-based framework to compare the two-dimensional profiles of the premaxilla in ventral aspect for a large sample of ruminant species. Our results suggest that, when a sample of browsing and grazing ruminants are classified ecologically based on a range of independent indicators of their feeding strategy, they cannot be fully discriminated on the basis of their premaxilla profile shape. Instead, our sample forms a shape variation continuum with overlap between groupings, but with a 78 percent chance of successful categorisation. Moreover, previously used terminology such as 'pointed' and 'blunt' are largely inadequate for delimiting snout shape varieties, insofar as these terms lack the descriptive power to define the morphological disparity demonstrated. These results suggest that previous attempts to use snout shape as a proxy for feeding style in ruminants may have been biased due to under-sampling of this highly diverse group and to lack of geometric rigour in the assessment of shape data. Alternatively, conflicting or inadequate evidence in defining 'browsers' and 'grazers' could have caused incorrect assignment to ecological groups, distorting our analyses. The relation between snout shape and body mass are also documented.

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Introduction

Members of Ruminantia are even-toed ungulate mammals defined uniquely by possession of a two-step digestion system involving the fermentation chamber in the foregut of the stomach, and by the presence of a reticulorumen, the structure from which the clade takes its name. Some 200 extant species are recognised currently [1]. Ruminant feeding strategies are reflected in their craniodental and gastrointestinal morphophysiological diversity, and have been conventionally categorised into 'browsers' and 'grazers', with an 'intermediate' sub-group [2-5]. Browsers are considered obligate non-grazers, but not vice-versa [2]. Some authors additionally include variants of frugivores, high-level browsers, and fresh grass grazers as independent categories in an attempt to encapsulate the full theoretical range of feeding strategies [3-5]. Variations in feeding strategy may also occur on different spatial and temporal levels, corresponding to environmental stresses (e.g., drought) [6], and plausibly a hierarchical grazing succession related to species' migration patterns, geomorphology, resource partitioning or forage quality [7-9].

Van Zyl [10] was the first to define a classification scheme for ungulates based on feeding strategy explicitly. Following this, Hofmann [11-16] extended Van Zyl's definitions to contain a novel qualitative morphological and physiological underpinning, specifically in ruminants relating to their particular ecological roles. This modified ungulate feeding classification scheme has been used widely in vertebrate (paleo)biology ever since its introduction. Nevertheless, this scheme's popularity is somewhat counter-intuitive insofar as, until recently, few studies have attempted to validate these widely-used categories within a robust quantitative framework through either empirical or heuristic analysis [17].

The typical dichotomy of 'browsers' and 'grazers' rests on a botanical foundation. Browsers typically consume berries and dicotyledonous leaves [11, 18, 19]. Grazers consume monocotyledonous grasses. Intermediate feeders vary their consumption preferences depending on season and geography [20, 21]. The putative morphological significance of this variation is that the physical, mechanical and biochemical properties of different forage types are adequate to drive and maintain a morpho-functional dichotomy among ruminant species that reflects the physical challenges they face accessing and/or processing different types of forage. It has been argued that these properties have exerted strong controls on the evolution of the masticatory apparatus and gastrointestinal tract [2], and specifically the reticulorumen physiology [22, 23] within ruminants.

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The botanical definitions of browsers and grazers have a complex history, with numerous authors unable to settle on a consistent threshold of forage consumption for either class. Several have regarded browsers as ruminants that consume < 10 percent grass, and grazers as those consuming > 90 percent grass per annum, with all other species being ranked as intermediate [24-27]. These authors provide little justification (or empirical evidence) for their stated thresholds. Conversely, others have selected > 75 percent grass per annum as the threshold criterion for their grazer class, and > 75 percent browse for browsers, again with little or no rationale provided [4, 28-30]. Clauss *et al.* [31] defined grazers as those consuming > 80 percent monocot material, and strict browsers as those with a "very low intake of monocot forage" (p. 399), while others used natural diet as a continuous variable [32]. In many other studies, feeding strategy delimitation has been based purely on qualitative assessments [33], where grazers are classified as those "consuming primarily grasses, sedges and other graminoids" (p. 178). This discordant usage is partially summarised in Clauss *et al.*, [17]. One study found that different thresholds of classification give different results in ecological analyses [34]; therefore this distinct lack of consistency is perplexing. Defining these thresholds in congruence with functional or ecological significance remains a problematic issue, one which is only exacerbated when they are used as a basis for further study into ruminant ecology.

There are numerous morphophysiological parameters that might, in theory, affect digestive rates and productivities, as well as masticatory efficiency, among ruminant species. However, the first anatomical feature (excluding perhaps the tongue and prehensile lips) that interacts with any and all types of ruminant forage is the snout or rostrum [35]. The anterior section of the snout is predominantly formed by the premaxillae. It is noted commonly that browsing ruminant species have pointed premaxillae and grazers a more squared or blunt shape representing a derived cropping condition [e.g., 24, 36]. Intermediate feeding strategies are posited to have an intermediate form, considered by some to conform to a mediolaterally compressed club-like shape [37]. Snout shape certainly is a prominent aspect of herbivore ecology, defining initial intake rate, chewing efficiency and forage selection ability [20, 38, 39, 40, 41]. That is, theoretically, a more pointed rostrum allows for increased selection sensitivity, whereas a wider or blunter form conforms to a more random cropping process with greater intake [24, 38]. Nevertheless, the claim that there is a close association between snout morphology and feeding strategy has rarely been subjected to formal hypothesis testing, and has not been subjected to a rigorous, geometry-based quantitative analysis, to date.

Several primary hypotheses used previously as foundations for the browser-grazer dichotomy have been rejected based on insufficient data, a lack of statistical support, or amendment based on more recent analyses [34, 42, 43]. Codron *et al*. [44] suggested that dietary variation occurs on a spatiotemporal scale for all browsers and grazers, and retains an intraspecific signal, conforming to Owen-Smith (1997) and Du Toit (2003) [33 and 45]. Regardless, there remains a lack of consensus regarding the ecological classification of ruminants by snout profile shape. Despite this, several distinctions are becoming apparent between browsing and grazing ruminants, and are supported within a statistical framework [17]. The principle aim of this investigation, then, is to determine whether empirically assessed patterns of snout shape variation in ruminants support the traditional distinctions that have been drawn between 'browser' and 'grazer' categories, and whether this approach allows a more precise morphological definition of these morpho-functional categories to be formulated. The statistical null hypothesis under consideration is that that snout profile shape exhibits no structured variation such that reliable morpho-functional categorization is possible.

Materials and Methods

Geometric morphometrics involves the multivariate statistical analysis of two- or three-dimensional Cartesian coordinate data, typically defined by discrete spatially-defined landmarks (i.e., topologically homologous loci on a structure [46]). Zoological studies are increasingly using a range of geometric morphometric techniques due to their intrinsic ability to analyse and guide interpretation of form in many different systematic contexts within a statistically coherent framework [47] (e.g., functional morphology, sexual dimorphism, ontogenic development, and phylogenetics). The ruminant specimen-set analysed here consisted of 121 different extant species, 115 of which were bovids or cervids as these are the most taxonomically diverse groups. Ruminant ecological categorizations were based on a number of sources and independent criteria, provided in S1. Ecological data could not be gathered for 27 of the analysed species, and were therefore inferred in accordance with their generic affinity (i.e., the same ecological class assumed for species of the same genus). This uncertainty is highlighted in S1. In 24 of these cases, this was not problematic, as all other members of the same genus occupied a single category. The remaining three cases were classed as 'intermediate' to make the fewest possible assumptions about their ecology (equivalent to 'unknown' group status). The within-genus similarity of group assignments made this a relatively simple process, but also imposes a slight but currently indeterminable phylogenetic bias upon the groupings (i.e., that members of the same genus will have similar ecologies based on their phylogenetic closeness, which is often based on morphology). It is assumed here that intraspecific shape differences will be less than interspecific shape differences; therefore, only a single specimen per species is necessary for the current investigation.

Snout profile outlines were digitally redrawn based on the initial photographs. The starting point for all the outlines was defined as the point (from a ventral aspect) where the suture between the maxilla and premaxilla intersects the left-lateral margin, ensuring that all subsequent semi-landmarks were interpolated to topologically homologous positions with respect to the total set of semi-landmarks used to represent the outline (each semi-landmark has a defined x-y position with respect to the co-ordinate system origin). Outlines were digitally transformed into geometric profiles using a chain of semi-landmarks collected from the images. One hundred equally spaced semi-landmarks were collected along each outline, a digitizing resolution sufficient to produce a geometrically faithful representation of the profiles. As the purpose of this investigation is to analyse pure shape variation in the peripheral margins of the sample premaxillae, no inferences can be made about the internal geometric structure of the snouts since they are not covered by the semi-landmarks.

These landmark data were subjected to a Procrustes (generalised least squares) transformation. Procrustes superimposition forms the core for analysis of pure shape, by removing the extraneous variation in scale, orientation and position for all specimens' semi-landmark constructions (see [48] and Box 2 of [49]). Optimising the fit of all specimens to each other was achieved by rigid rotation iteration until the distance between successive mean landmark configurations fell below 0.0001. This provided the ability for progression of analysis in shape space as opposed to form space. The specimens at this stage were sub-divided into their sub-groupings for each subsequent analysis.

Superposed co-ordinate data for defined browsers and grazers were subject to a covariance-based principal components analysis (PCA) [50], which preserves the Procrustes distances among specimens [46]. Four principal component (PC) axes accounted for greater than 95 percent of the total variance, with the first two axes accounting for more than 88 percent (S1).

Accordingly, projected scores on these four PC axes were retained and served as the basis for secondary analysis. These principal component scores were then subjected to a canonical variates analysis (CVA) [51]. This multivariate technique transforms the data to a configuration that achieves the optimal discrimination between group centroids relative to the group dispersion structure [49, 51, 52] (S2). A X^2 likelihood ratio test was performed to test group distinctiveness (i.e., group dispersion structure) of the data, with respect to the sample that defines the discriminant space [53]. The resulting X^2 probability represents a validation test of the between-groups covariance structure; i.e., a low probability (<0.05, traditionally) reflects a statistically significant difference in the dispersion structure with respect to the defined groups. This implies that the group distributions are the products of some extrinsic factor, such as biogeography, phylogeny, functional constraints, or ecology, as opposed having a stochastic distribution.

To represent a shape transformation sequence through the data based on hypothetical successive models of the snout profiles in a space defined by maximum between-groups shape variation, overlay or 'strobe plot' comparisons of modelled snout shapes were performed [54]. The number of orthogonal canonical variates axes corresponding to the number of pre-defined groups minus one (i.e., the minimum number of axes required to demarcate groups), with five modelled points per axis, were back-projected into the space of the raw principal components [51]. These points represent the two extreme points, the central point, and two medially-interpolated points between these on the CV axes. The result is a set of non-orthogonal canonical variates (i.e., discriminant axes) oriented with respect to the data within Procrustes-scaled PCA space. Each model axis was plotted in order to illustrate and assess the models of shape variation represented along the CV axes [54].

This process of dimensionality reduction, discriminant analysis, dispersion structure validation, and model visualisation provides a statistically rigorous protocol for assessing the validity of the ruminant feeding categories. The relationships between body mass and snout morphology were then investigated, with body masses extracted from the PanTHERIA database (S3), using snout centroid size as a proxy for size.

Results

Principal Components Analysis

Four principal components axes explained more than 95 percent of the total snout outline shape variance within the browser-grazer dataset (PCA Eigenvalues tab in S1), with the first two of these explaining the overwhelming majority of this percentage (88%). These two axes can be used to define a low-dimensional shape ordination space (Fig. 1). Grazer species appear relatively confined in this PC space relative to browsers. The two groups overlap about the region of the grand mean, but occupy distinct regions of the principal components space; browsers score more positively on both axes, while grazers occupy the more negative spaces.

Figure 1. PCA score plot for ruminants classified according to feeding strategy. Ecological classifications are given in S1. The convex hulls represent a morphospace constrained by the extreme data points within the range envelope. Scores for the species used to define this space are in the PCA scores tab of S1.

The 'unknown' ruminants were projected into this browser-grazer defined subspace to see where their shapes fell in a space defined by known categories (Fig. 2). Generally, the unknowns occupy a broad central region that falls dominantly within the browser space, and exhibits only marginal overlap with the grazers. There is a greater range of morphospace occupation in both PC-1 and PC-2, suggesting higher variability than the grazers. Compared to browsers, the space occupation is more similar, suggesting that there is an analogous shape and shape range between the unknown group and the known browsers. There is still significant overlap about the grand mean, suggesting that within all ruminants, there is a tendency for all snout shapes, irrespective of feeding strategy, to converge on the mean shape of all the sampled ruminant species.

Figure 2. PCA score plot for ruminants classified according to their feeding strategy, with 'intermediates' projected into the space.

Canonical Variates Analysis

The PCA scores on the first four axes were subjected to a CVA. As there are only two groupings, the first CV axis explains 100% of the variance between the group centroids, with the second CV axis purely a construct to form a two-dimensional ordination. Browsers and grazers occupy similarly overlapping canonical variate (CV) space regions. Grazers occupy a broad region, occupying lower values along the CV-1 axis (see S2 for associated CVA scores). The overlapping nature of these two groups implies that the within-groups shape variation is distributed in a manner such that there is a complete snout profile continuum between these two ecological groups (Fig. 3). Nevertheless quasi-distinct discriminant spaces can still be identified. A likelihood ratio test [55] of the separation of group means relative to their within-group dispersions results gives the result of 0.0 (Distance matrix tab of S2), a value confirmed using Markov Chain Monte Carlo and bootstrapping simulations of the log-likelihood ratio distribution (1000 pseudoreplicate iterations each). This indicates that the likelihood of these groups occupying their positions in the overall CV space as a result of the effect of random sampling of a single, underlying population is well below the standard level of statistical significance. Accordingly, the alternative hypothesis — that the observed magnitude of centroid separation is such that these data were likely drawn from different shape populations with different characteristics — is accepted.

Figure 3. Browsers and grazers in canonical variates space. The occupation of distinct discriminant spaces is clear, although not absolute.

The unknown sub-group was projected into this defined space (Fig. 4). This provides a visualisation of which group on a species-by-species basis the unknowns are more likely to be assigned to. Quantitatively, this is provided in the Distance Matrix tab of S2, where the distances from each unknown species to the known-group means is given, and assignment to either browsers or grazers based upon this. Of the 48 unknown species, 12 are assigned to the grazer category, and 36 to browsers, for a total of 44 and 74 respectively (or 37.28 and 62.71 percent).

The confidence level of this is provided by calculation of a confusion matrix (S2), which summarizes the percent of correct assignment of species with respect to their *a priori*-defined groups based on their distances to the respective group means in the canonical variates space.

The result indicates that in almost 4 out of every 5 cases (78.57%), the correct assignment of a species to its feeding class, based on secondary criteria, is possible using snout shape. A jackknifed estimate of the performance of this discriminant space produced similar results, with only an additional two browsers being incorrectly identified as grazers for a total correct estimate percentage of 75.71% (S2).

Figure 4. CVA score plot for ruminants classified according to their feeding strategy, with 'intermediates' projected into the space.

To interpret the geometric character of between-groups shape deformation axis was modelled using five points coordinate points along the CV-1 axis: the mean, two distal points, and interpolated medial points between these three. This single axis was back-projected into its corresponding PC-space and the semilandmark point configuration reconstructed using the method of MacLeod [54, 56]. A 'strobe plot' of these models shows the progressive deformation from one end of the shape spectrum within the maximum shape envelope described by the specimens' premaxillae (Fig. 5). The pattern of shape variation described by this axis clearly cannot be described as a continuum from 'blunt' to 'pointed'. This axis shows progressive deformation of the premaxilla, from a rostrolaterally widened, laterally compressed, and distally depressed geometry into a laterally expanded, rostrolaterally constricted, and distally thinned and pointed shape. A transition from blunt to pointed is little more than an over-simplified caricature of the true character of deformation sequence. This initial conclusion may have been reached as it does indeed represent an aspect of the deformation sequence, and describes it in a simple way. Use of the approach here, however, gives analysts access to the total range of shape variation expressed by canonical variates axes, and provides an appreciation of the complexity of form within the data.

Figure 5. Strobe plots of the CV model axes in PC space for browsers and grazers. The right-hand column is an overlay plot, showing the progressive geometric deformation between model points on each axis.

Taken as a whole, these results suggest that snout shape is largely sufficient to differentiate between - and so to identify - different feeding classes in ruminants. An additional implication is that snout shape is concordant with other putative functional traits used to distinguish between the feeding types (e.g., the hypsodonty index, percentage of grass in diet), or that there is some subsidiary function that it serves. It is also apparent that ruminants are so morphologically diverse, and have adapted to maximise resource exploitation in their respective ecosystems, that they exhibit widespread morphological convergence in snout profiles, forming a continuum of shape variation with each particular species occupying a defined point relating to a specific suite of ecomorphological characteristics.

The relationships between body mass scaling and feeding style have received considerable attention before with ruminants (e.g., [40]). Snout shape plays a role in defining intake rate, which may relate to body mass [39]. Accordingly, body mass data were extracted from the PanTHERIA database (S3), and compared with snout centroid size as a proxy for morphology in browsers and grazers. Species highlighted in bold (in the extended tab) are those whose ecology was classed as 'unknown' prior to assignment via the distance matrix. These were initially excluded for the first run of this analysis, and then added to the second. Centroid sizes of the landmark configurations can be used as shape-independent and dimensionless measures of size in samples, and a general proxy for morphology. Primary data were confirmed to conform to a Gaussian distribution with the Shapiro-Wilk test using the program PAST (Palaeontological Statistics; p = 0.9645). Pearson's test (r = 0.165) demonstrates that body mass and centroid size are only very weakly correlated (Fig. 6). This implies that feeding style is largely independent of body mass, based on the inferred relationship between snout morphology and feeding style. Additionally, this analysis suggests that browsers occupy a broader range of body sizes and disparity of morphologies compared to the more restricted grazing species. When the additional data were included, the pattern remained largely the same, except with slightly larger group dispersion structures (Extended tab in S3). These extended data were confirmed again by the Shapiro-Wilk test (p = 0.9863), with Pearson's test indicating a slightly stronger, but still weak correlation between the two variables (r = 0.23438). Looking at individual groups, browsers seem to exhibit a slight positive allometry between body mass and snout centroid size, with grazers showing a slight negative correlation. However, this relationship in grazers is reversed into a weak positive correlation in the extended analysis involving 'unknown' species classified as grazers (S3). In all cases, the strength of these relationships is weak, based on simple R^2 calculations.

Figure 6. Relationship between log-transformed centroid size and body mass in browsing and grazing ruminants.

Discussion

The history of ruminant ecological classification is convoluted, with only marginal progress over time toward clarity or consensus. Based initially on a simple botanical underpinning, the problem became increasingly multifaceted as new functional 'traits' were exposed with new methods of analysis, and new theoretical revisions. This problem can be stated as what, if any, is the best method of classifying ruminants in a functional ecological framework, and what will be the parameters that define these discrete classes.

Previous work assessing this problem in the context of snout shape [37, 57] has followed the methodology of Walker [58], using it primarily to aid reconstruction of palaeodiets in ruminants. These assessments were based on quantitative interpretation of exemplar taxa, with the method requiring construction of the anterior snout curve using a cubic spline-fit function framed to assess intraspecific variation. This method uses a somewhat arbitrary system of vectors to encapsulate the majority of premaxillary shape variation. These authors used photographs in dorsal aspect stating that there was "no homologous point" on the premaxillary outline (p. 1063 of [37]). This is why the ventral aspect should be analysed (as here), due to the easily traceable premaxillary-maxillary suture along with the fact that this is the interactive surface of the oral aperture. However, the main drawback of their method is that the *a priori* classification of specimens into functional feeding guilds - with no statistical testing or evidence-based support for assignment - inevitably introduced a large degree of subjectivity into the mean shape and shape variation calculations. Classification should ideally be determined a posteriori, once distinct variations between sub-groups have been discovered, if it all. For example, in Figure 3 of Solounias *et al.*, (1988; [35]), the intermediate shape looks considerably skewed towards the grazer class shape. The reproduced images only serve to emphasize the imprecision of already arbitrarily bound categories. Moreover, their mean shapes are not a useful guide to classification due to the obviously overlapping shape-range envelopes. The statistics provided in Table 1 of [35] confound matters further as their intermediate sample is clearly more similar to grazers than browsers. This is likely due to the treatment of the intermediate sub-group as a taxonomic 'waste-basket', where species that don't conform to either browsing or grazing categories are assigned depending on which trait or suite of traits are being analysed, with little consideration on to the ecological basis for the assignment. This approach to ecological classification is at odds with the otherwise well-understood browsing and grazing ecological categories,

Other authors have identified snout width as a proxy for distal snout shape, with measurements taken at the ventral maxilla-premaxilla intersection on the lateral margin [24, 36]. When describing the geometry of complex shapes a single linear metric is usually inadequate as equal measurements can often describe completely disparate geometries of varying complexity, and non-comparable function. These authors used this measurement, along with the palatal width, to define a 'relative muzzle width ratio', which they used to represent the ratio between body size and the oral aperture, as well as possibly representing oral intake and processing rate (note that 'muzzle' describes the flesh covering the snout, not the cranial bones, as is misconstrued here). Most modern morphometricians agree that a ratio is a poor shape measure when used singularly, since all a ratio can represent adequately is an ellipse, if the two measurements represent orthogonal axes, as in the method used [59]. This approach may be sufficient for partially representing extremes of the 'browser' end of the shape spectrum, but can just as easily describe a blunt form, as grazers are postulated to have. The set of shapes the same ratio can represent can be infinitely complex. For example, imagine trying to model a sinusoidal crenulation with a two-dimensional ratio. Hence, ratios are inappropriate proxies for snout shape characterisation (contra [24]). Ratios will also almost always fail to account for the ubiquity of allometric growth patterns in organisms. A general relationship between muzzle width and the defined dietary categories was discovered [24], if not entirely faithful.

The principle hypothesis of this study was that snout profile shape forms discrete varieties that covary between independent feeding strategies, in accordance with numerous previous studies [24, 35, 36, 41]. The null hypothesis relates to the conclusions of Pérez-Barbéria and Gordon [29], among others, that feeding strategy is incongruent with premaxilla morphology. One alternative hypothesis is that the shape of specimen snouts forms a continuum, with 'browser-type' and 'grazer-type' morphologies comprising the end-members. This hypothesis is based on the inference that classifying what are intrinsically morphologically diverse organisms into discrete clusters is problematic and somewhat counter-intuitive, if purely for the purposes of having an antecedent framework onto which new hypotheses of functional morphology can be built. Our analysis shows that, when ruminants are classified ecologically as browsers and grazers, based on a range of secondary criteria, they cannot be fully discriminated based on the shape of their premaxillary profile, a result inconsistent with previous investigations of this issue in which the dichotomy was considered to be absolute [24, 35, 36, 41]. Snout shape is moderately homoplastic in nature, with a broad range of profile geometries being present in both of the feeding-style sub-groups. Despite exhibiting a degree of shape overlap, these groups retain moderate geometric independence, such that they can be assigned to the correct groups almost 80 percent of the time. While profile-based classification is not perfect, it has potential use for fossil ruminants, in that it enables quantitative assessment of inferring their ecologies as well as providing a means of estimating the statistical confidence that can be assigned to these inferences.

The results obtained by this study also suggest a new mode of analysis for future investigations of functional ecology in ruminants, by using multivariate statistical analysis combined with tests of confidence to assess the validity of naturally-occurring groups. A similar conclusion was reached by Pérez-Barbería *et al*. [60], in that the current boundaries between ruminant feeding strategies remain somewhat arbitrary. A viable approach to resolving this problem should employ a covariate or group of covariates as continuous variables, with thresholds being based on the identification of functionally significant and discrete clusters. However, authors who have investigated this issue so far with this methodology have found no morphological discrepancies that can explain variation in ruminant digestive efficiency based on digestive, not ingestive, morphology [2, 19, 32, 61]. This perplexing result may, in part, be due to treating species as static entities, when realistically thresholds should be constructed on a sliding scale accounting for population and spatiotemporal variations where appropriate [33]. It also seems that general patterns must be flexible enough to account for singular exceptions (e.g., frugivores) and are currently insufficient to encapsulate the full diversity of ruminant feeding habits. The real problem, however, may stem from the fact that previous work has attempted to arbitrarily sub-divide and categorise species that, in reality, form a continuum, with 'browsers' and 'grazers' occupying terminal points on the continuum, representing the most stationary, specialised, or inflexible feeding types. This scenario is most likely the one supported by the results of our investigation.

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Theoretically, a higher food intake rate should drive covariation within the mandible, forcing the evolution of stronger anatomical structures [62] (e.g., strengthening or fusion of sutures, increased muscle attachment area, and decreasing pleurokinesis and increased resistance to strain). This inference does not necessarily suggest that, as snout shape and hence intake rate, varies, it forces covariation of other morphophysiological parameters. Rather, it simply controls the initial parameter with which all other functional domains interact. This suggestion of covariation by Janis *et al*. [62] was corroborated by Fletcher *et al*. [63] in determining that evolution of the masticatory apparatus has a functional or adaptational origin, challenging other studies which identified it as being a phylogenetic artefact [29, 36, 64, 65]. This hypothesis requires further investigation, with snout shape being analysed to assess functional significance as a trait affecting both intake rate (volume per unit of time) and selectivity (non-parametric), and plausibly maximum bite size (volume) [66, 67].

Conclusions

Using a two-dimensional representation of the ruminant snout in ventral aspect, it is demonstrated that there is a strong relationship between snout shape and feeding ecology within a highly diverse sample of the major ruminant clades, but only when the data set is restricted to members of the relatively well-defined browser and grazer classes. This between-group discrimination is statistically significant as assessed by a likelihood ratio test, and is also largely independent of body mass.

It is further apparent that previous categorisations, which included putative 'intermediates', snout shapes relative to feeding strategy, are inadequate in their depictions of the full range of exhibited morphological variation (i.e., 'browsers' do not strictly have 'pointed' snouts, and 'grazers' do not just have 'blunt' snouts as asserted previously by many authors). The geometric complexity of this snout morphology is more extensive than this and forms a continuum of shape variation. Our results suggest that attempts to place thresholds on other related factors involved in feeding are problematic and quantitative testing is required *a priori* (following the recommendations of Gordon, [34]).

In light of these results, inferences made by [62] - that intake rate forces covariation in the anatomical strength of the mandible - should be reanalysed to determine whether grazing ruminants genuinely have a more robust masticatory apparatus than browsing ruminants, or whether this conclusion is based on a biased appraisal of the relation between snout shape and the ingestive apparatus in a group-defining context. In contrast, we suggest, in a manner analogous to that of Codron *et al*. [44], that ruminant diets represent a continuum with variation explicitly occurring on a spatiotemporal (geographical and seasonal) scale for all feeding strategies. Furthermore, snout shape appears to be highly convergent, with a range of different ruminants having similar profile shapes. This requires additional analysis in terms of ruminant phylogenetic affinity, [68, 69, 70], species' ranges, and additional significant ecological parameters.

The fact that feeding strategy-based categories were demonstrated to be associated with snout shape in this investigation offer a model for future ecological studies regarding the reconstruction of palaeodiets using this dataset to delimit and identify extinct browsing and grazing species [35, 37]. This aspect of palaeoecology could feasibly be integrated with additional indicators of diet, such as isotopic signatures and microwear in teeth [71, 72], or the hypsodonty index [73].

It is conceivable that our results are the product of a lack of consistency in defining functional feeding groups for ruminants with respect to other morphophysiological traits. The functional significance of snout shape in relation to bite size, intake rate, and selectivity is not explicitly addressed by our study. Indeed, our results indicate that closer inspection of these relationships is required. Quantitative metrics describing both of these ecologically significant parameters should provide a firm basis for these anticipated future studies [66].

What is undoubtedly necessary in future studies is the dissection of recovered signals to determine what proportion of trait covariation can be explained by phylogenetic relationships [64, 65]. Applicable methods include the phylogenetic modelling, which has gained increasing interest in the integration of ecology and macroevolution [74]. This will facilitate the teasing apart of genuine adaptational signals as opposed to morphological similarity based on common ancestry. Furthermore, if singular or multiple functional traits are found to be phylogenetic artefacts, it may be possible to track the sequence of acquisition, and therefore trace the ecological coevolution of ruminants. In addition to phylogeny, other factors such as ontogeny, body mass, and sexual dimorphism should be scrutinised within a statistical framework to detect potential allometric variation, and possible synchronisation of trait acquisition and evolution patterns between sexes.

Supporting Information

Table S1 Categorical data used for all analyses, PCA eigenvalues, and PCA scores (.xls).

Table S2 CVA scores, confusion matrix, distance matrix, and jackknifed confusion matrix (.xls).

Table S3 Body mass and centroid size data (including extended analysis; .xls).

All snout profiles used in this study have been uploaded to Fig**share** (keywords: ruminants, snout, profile, outline).

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Figure 1

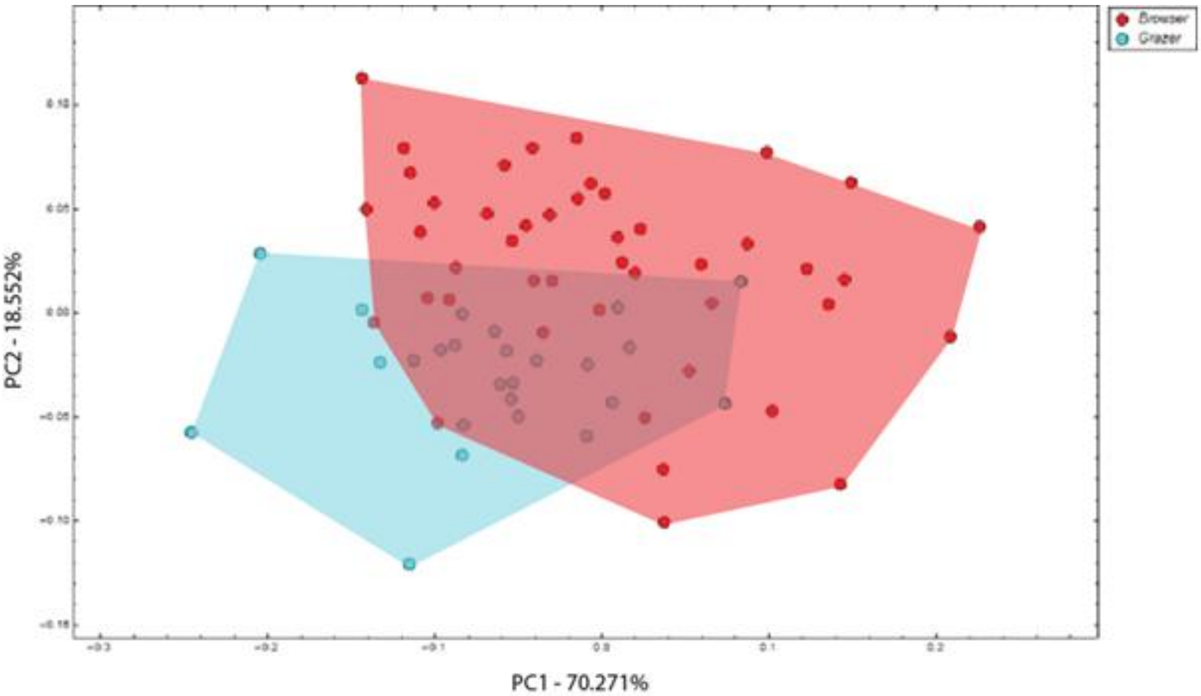
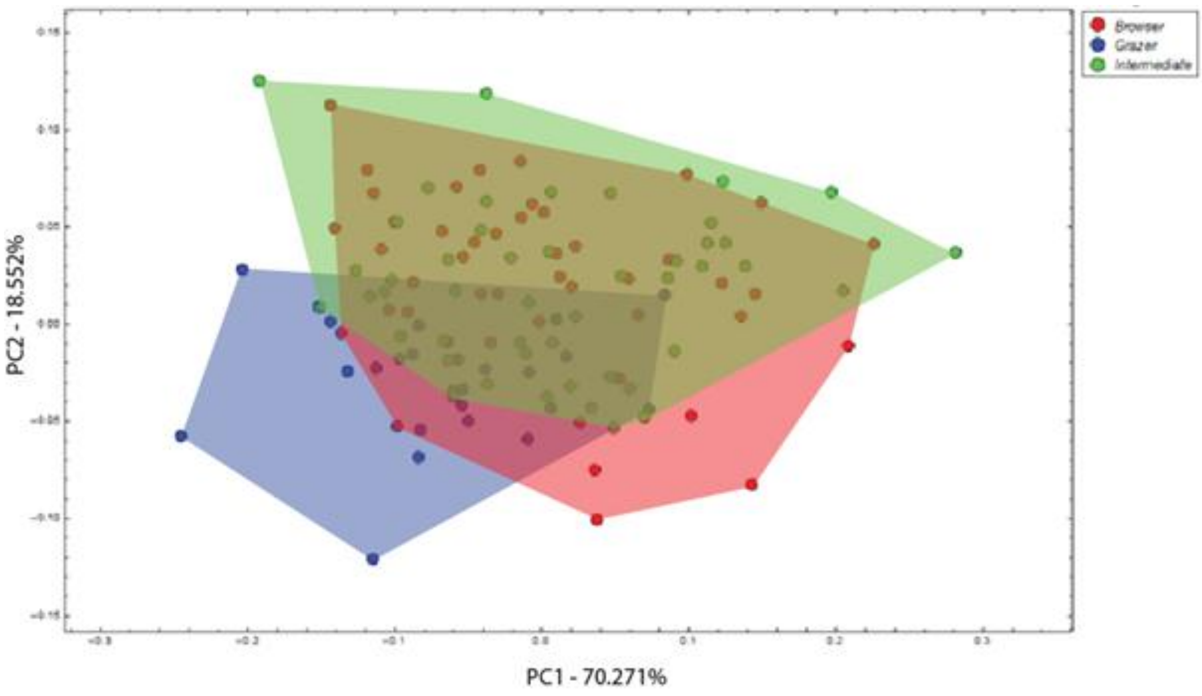


Figure 2



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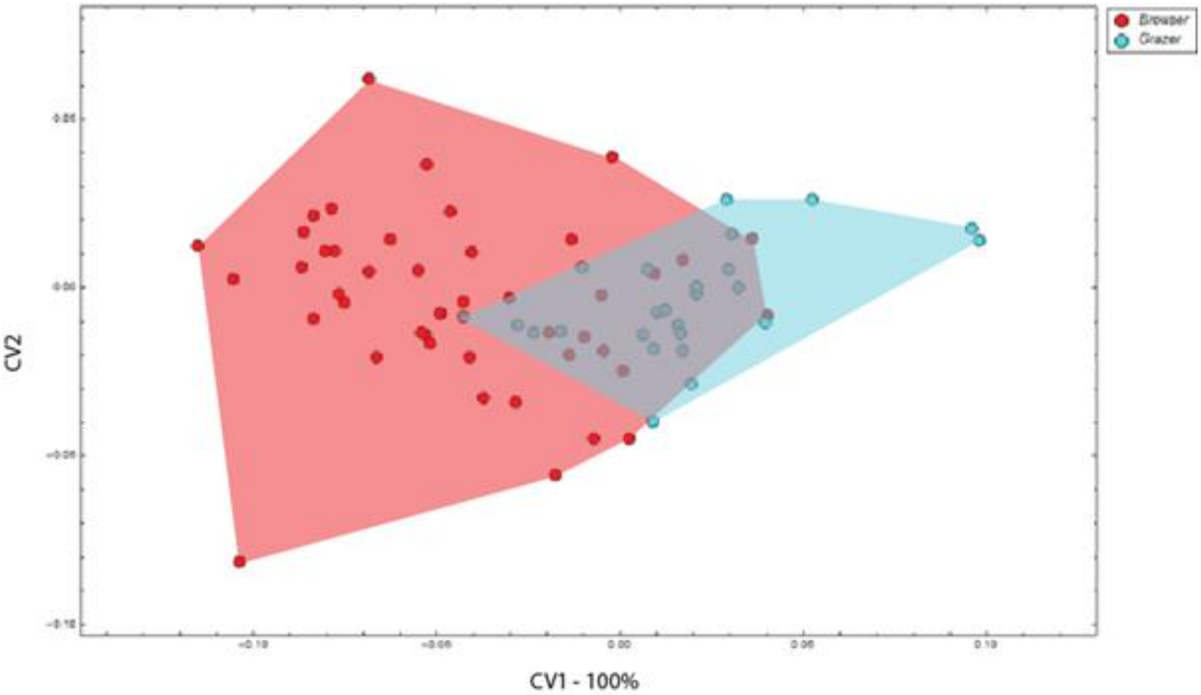

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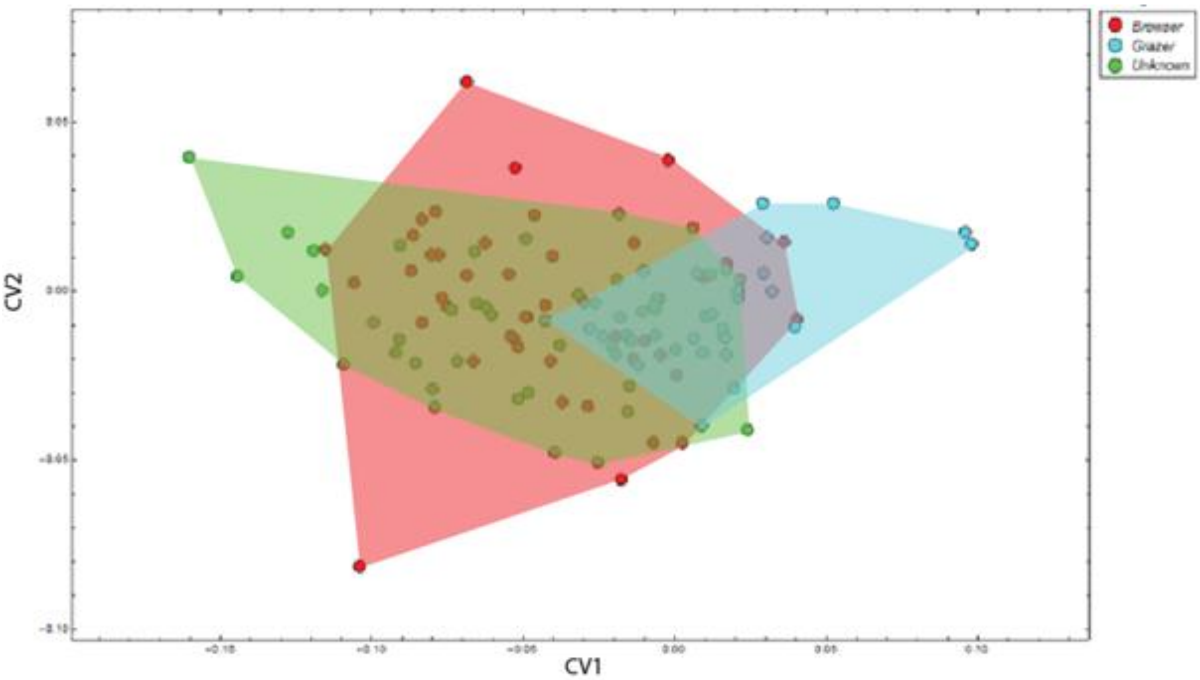

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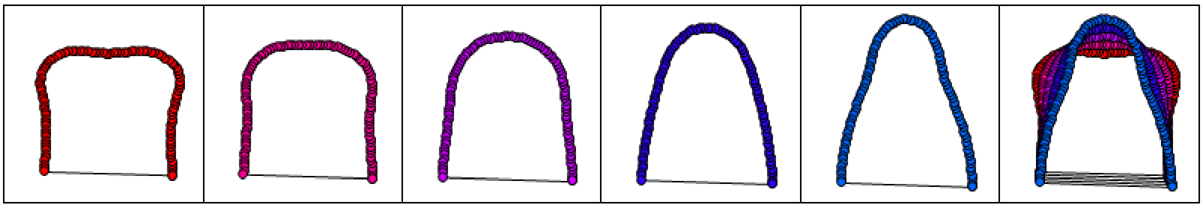
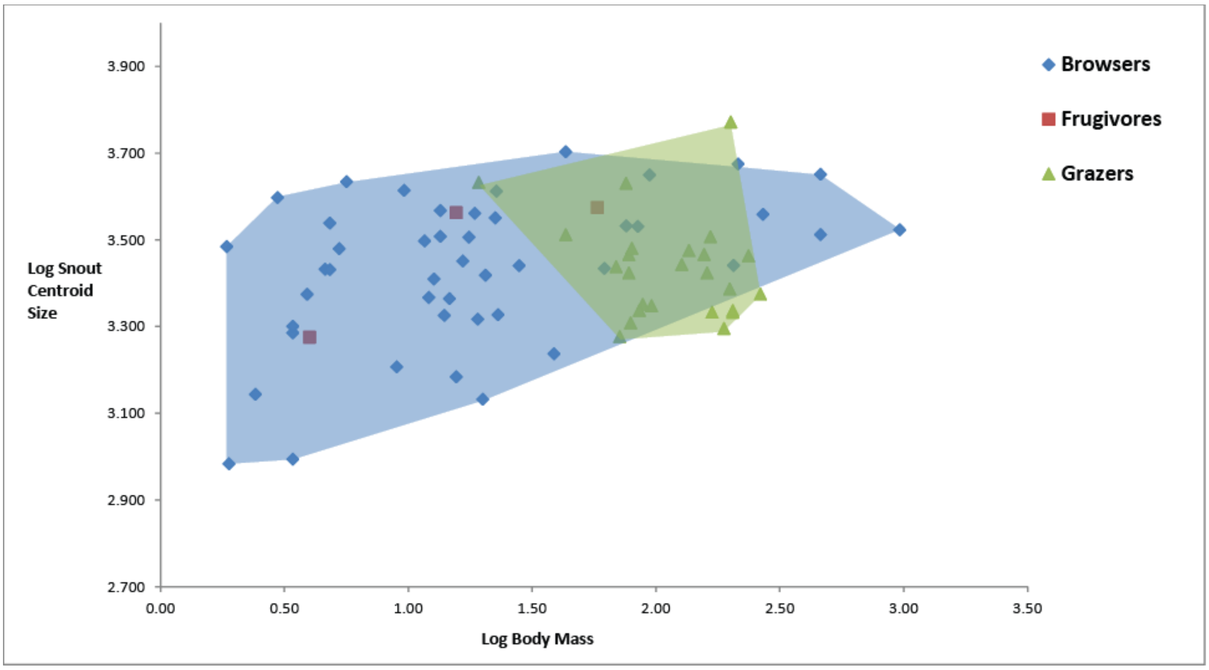


Figure 6



Supplementary Information – Table 1, tabs 1, 2, and 3

Family	Subfamily	Genus	Species	Sub-species	Common Name	Ecology	Criterion	Reference
Antilocapridae	-	*Antilocapra*	*americana*	-	Pronghorn	Intermediate	Unknown	75
Bovidae	Aepycerotinae	*Aepyceros*	*melampus*	-	Impala	Intermediate	Hypsodonty	76
Bovidae	Alcelaphinae	*Alcelaphus*	*buselaphus*	*major*	Hartebeest	Grazer	>75% grasses	40
Bovidae	Alcelaphinae	*Beatragus*	*hunteri*	-	Hirola	Grazer	Various	77
Bovidae	Alcelaphinae	*Connochaetes*	*gnou*	-	Black Wildebeest	Grazer	>75% grasses	40
Bovidae	Alcelaphinae	*Connochaetes*	*taurinus*	*johnstoni*	Blue Wildebeest	Grazer	90% grasses	78
Bovidae	Alcelaphinae	*Damaliscus*	*albifrons*	-	Bontebok	Grazer	Generic affinity	Inferred
Bovidae	Alcelaphinae	*Damaliscus*	*dorcas*	-	Blesbok	Grazer	Various	77
Bovidae	Alcelaphinae	*Damaliscus*	*korrigum*	-	Korrigum	Grazer	>75% grasses	40
Bovidae	Alcelaphinae	*Damaliscus*	*liechtensteinii*	-	Liechtenstein's Hartebeest	Grazer	Generic affinity	Inferred
Bovidae	Alcelaphinae	*Damaliscus*	*lunatus*	-	Topi	Grazer	Hypsodonty	76
Bovidae	Alcelaphinae	*Damaliscus*	*pygargus*	-	Bontebok	Grazer	>80% grasses	79
Bovidae	Antilopinae	*Ammodorcas*	*clarkei*	-	Dibatag	Browser	Various	77
Bovidae	Antilopinae	*Antidorcas*	*marsupialis*	*angloensis*	Springbok	Intermediate	30% grasses	78
Bovidae	Antilopinae	*Antilope*	*cervicapra*	-	Blackbuck	Intermediate	Mesodonty	76
Bovidae	Antilopinae	*Dorcatragus*	*megalotis*	-	Beira	Intermediate	Various	77
Bovidae	Antilopinae	*Eudorcas*	*thomsoni*	-	Thomson's Gazelle	Intermediate	Hypsodonty	76
Bovidae	Antilopinae	*Gazella*	*spekei*	-	Speke's Gazelle	Intermediate	50% grasses	78
Bovidae	Antilopinae	*Gazella*	*bennettii*	-	Indian Gazelle	Intermediate	Generic affinity	Inferred
Bovidae	Antilopinae	*Gazella*	*cuvieri*	-	Cuvier's Gazelle	Intermediate	Generic affinity	Inferred
Bovidae	Antilopinae	*Gazella*	*dama*	*ruficollis*	Dama Gazelle	Intermediate	47.5% grasses	78
Bovidae	Antilopinae	*Gazella*	*dorcas*		Dorcas Gazelle	Intermediate	Various	77
Bovidae	Antilopinae	*Gazella*	*gazella*	*arabica*	Mountain Gazelle	Intermediate	Mesodonty	76
Bovidae	Antilopinae	*Gazella*	*leptoceros*	-	Rhim Gazelle	Intermediate	Generic affinity	Inferred
Bovidae	Antilopinae	*Gazella*	*rufifrons*	-	Red-Fronted Gazelle	Intermediate	Generic affinity	Inferred
Bovidae	Antilopinae	*Gazella*	*saudiya*	-	Saudi Gazelle	Intermediate	Generic affinity	Inferred
Bovidae	Antilopinae	*Gazella*	*soemmeringi*	-	Sömmering's Gazelle	Intermediate	50% grasses	78
Bovidae	Antilopinae	*Gazella*	*subgutturosa*	-	Goitered Gazelle	Intermediate	50% grasses	78
Bovidae	Antilopinae	*Litocranius*	*walleri*	-	Gerenuk	Browser	>75% browse	28
Bovidae	Antilopinae	*Madoqua*	*cordeauxi*	-	Cordeaux's Dik-Dik	Browser	Concentrate selector	14
Bovidae	Antilopinae	*Madoqua*	*phillipsi*	-	Phillip's Dik-Dik	Browser	Concentrate selector	14
Bovidae	Antilopinae	*Madoqua*	*saltiana*	*erlangeri*	Salt's Dik-Dik	Browser	10% grasses	78
Bovidae	Antilopinae	*Madoqua*	*swaynei*	*piacentinii*	Silver Dik-Dik	Browser	Concentrate selector	14
Bovidae	Antilopinae	*Nanger*	*granti*	-	Grant's Gazelle	Intermediate	Hypsodonty	76
Bovidae	Antilopinae	*Neotragus*	*batesi*	-	Dwarf Antelope	Browser	Generic affinity	Inferred
Bovidae	Antilopinae	*Neotragus*	*moschatus*	-	Suni	Browser	>75% browse	28
Bovidae	Antilopinae	*Neotragus*	*pygmaeus*	-	Royal Antelope	Browser	Various	77
Bovidae	Antilopinae	*Oreotragus*	*oreotragus*	-	Klippspringer	Browser	5% grasses	78
Bovidae	Antilopinae	*Ourebia*	*ourebi*	-	Oribi	Intermediate	Hypsodonty	76
Bovidae	Antilopinae	*Procapra*	*gutturosa*	-	Mongolian Gazelle	Intermediate	28% grasses	78
Bovidae	Antilopinae	*Procapra*	*picticaudata*	-	Tibetan Gazelle	Intermediate	Generic affinity	Inferred
Bovidae	Antilopinae	*Procapra*	*przewalskii*	-	Przewalski's Gazelle	Intermediate	Generic affinity	Inferred
Bovidae	Antilopinae	*Raphicerus*	*campestris*	-	Steenbok	Browser	>75% browse	40
Bovidae	Antilopinae	*Raphicerus*	*melanotis*	-	Cape Grysbok	Intermediate	Various	77
Bovidae	Antilopinae	*Raphicerus*	*sharpei*	*colonicus*	Sharpe's Grysbok	Intermediate	Generic affinity	Inferred
Bovidae	Antilopinae	*Rhynchotragus*	*damarensis*	*variani*	Domore's Dik-Dik	Browser	Concentrate selector	14
Bovidae	Antilopinae	*Rhynchotragus*	*kirkii*	*minor*	Kirk's Dik-Dik	Browser	>75% browse	40
Bovidae	Antilopinae	*Rhynchotragus*	*guentheri*	*hadsoni*	Gunther's Dik-Dik	Browser	Various	77
Bovidae	Bovinae	*Boselaphus*	*tragocamelus*	-	Nilgai	Intermediate	Mesodonty	76
Bovidae	Bovinae	*Taurotragus*	*oryx*	-	Eland	Intermediate	Various	77
Bovidae	Bovinae	*Tetracerus*	*quadricornis*	-	Four-Horned Antelope	Grazer	Hypsodonty	76
Bovidae	Bovinae	*Tragelaphus*	*angasii*	-	Nyala	Intermediate	Various	77
Bovidae	Bovinae	*Tragelaphus*	*buxtoni*	-	Mountain Nyala	Browser	Various	77
Bovidae	Bovinae	*Tragelaphus*	*eurycerus*	-	Bongo	Browser	Brachydonty	76
Bovidae	Bovinae	*Tragelaphus*	*imberbis*	-	Lesser Kudu	Browser	Brachydonty	76
Bovidae	Bovinae	*Tragelaphus*	*scriptus*	-	Bushbuck	Browser	Various	77
Bovidae	Bovinae	*Tragelaphus*	*spekii*	-	Sitatunga	Intermediate	Mesodonty	76
Bovidae	Bovinae	*Tragelaphus*	*strepticeros*	-	Greater Kudu	Browser	Various	77
Bovidae	Caprinae	*Pseudois*	*nayaur*	-	Bharal	Intermediate	Various	77
Bovidae	Cephalophinae	*Cephalophus*	*dorsalis*	-	Bay Duiker	Browser	Brachydonty	76
Bovidae	Cephalophinae	*Cephalophus*	*harveyi*	*ignifer*	Harvey's Duiker	Browser	1% grasses	78
Bovidae	Cephalophinae	*Cephalophus*	*maxwelli*	-	Maxwell's Duiker	Browser	Generic affinity	Inferred
Bovidae	Cephalophinae	*Cephalophus*	*monticola*	*schultzei*	Blue Duiker	Frugivore	Unknown	75
Bovidae	Cephalophinae	*Cephalophus*	*natelensis*	*natelensis*	Natal Duiker	Browser	1% grasses	78
Bovidae	Cephalophinae	*Cephalophus*	*niger*	-	Black Duiker	Browser	Brachydonty	76
Bovidae	Cephalophinae	*Cephalophus*	*nigrifrons*	-	Black-Fronted Duiker	Browser	Generic affinity	Inferred
Bovidae	Cephalophinae	*Cephalophus*	*rufilatus*	-	Red-Flanked Duiker	Browser	Concentrate selector	14
Bovidae	Cephalophinae	*Cephalophus*	*silvicultor*	*ruficristus*	Yello-Backed Duiker	Browser	Generic affinity	Inferred
Bovidae	Cephalophinae	*Cephalophus*	*zebra*	-	Zebra Duiker	Browser	Generic affinity	Inferred
Bovidae	Cephalophinae	*Sylvicapra*	*grimmia*	-	Bush Duiker	Frugivore	Various	77
Bovidae	Hippotraginae	*Addax*	*nasomaculatus*	-	Addax	Grazer	80% grass	78
Bovidae	Hippotraginae	*Hippotragus*	*equinus*	-	Roan Antelope	Grazer	Hypsodonty	76
Bovidae	Hippotraginae	*Hippotragus*	*niger*	-	Sable Antelope	Grazer	Various	14
Bovidae	Hippotraginae	*Oryx*	*beisa*	*beisa*	Beisa	Grazer	>75% grasses	28
Bovidae	Hippotraginae	*Oryx*	*gazella*	-	Gemsbok	Grazer	82% grasses	78
Bovidae	Hippotraginae	*Oryx*	*leucoryx*	-	Arabian Oryx	Grazer	Grass/roughage eaters	14
Bovidae	Reduncinae	*Kobus*	*defassa*	-	Defassa Waterbuck	Grazer	Hypsodonty	76
Bovidae	Reduncinae	*Kobus*	*ellipsiprymnus*	-	Waterbuck	Grazer	Hypsodonty	76
Bovidae	Reduncinae	*Kobus*	*kob*	*leucotis*	Kob	Grazer	Various	77
Bovidae	Reduncinae	*Kobus*	*leche*	-	Lechwe	Grazer	Hypsodonty	76
Bovidae	Reduncinae	*Kobus*	*megaceros*	-	Nile Lechwe	Grazer	Generic affinity	Inferred
Bovidae	Reduncinae	*Kobus*	*vardonii*	-	Puku	Grazer	Various	77
Bovidae	Reduncinae	*Pelea*	*capreolus*	-	Grey Rhebuck	Browser	7% grasses	78
Bovidae	Reduncinae	*Redunca*	*arundinum*	-	Southern Reedbuck	Frugivore	Various	77
Bovidae	Reduncinae	*Redunca*	*fulvurofula*	-	Mountain Reedbuck	Intermediate	Various	77
Bovidae	Reduncinae	*Redunca*	*redunca*	-	Bohar Reedbuck	Grazer	Hypsodonty	76
Cervidae	Capreolinae	*Alces*	*alces*	-	Moose	Browser	<20% grasses	79
Cervidae	Capreolinae	*Alces*	*palmatus*	-	Moose	Browser	Concentrate selector	14
Cervidae	Capreolinae	*Blastoceras*	*bezoarticus*	-	Pampas Deer	Intermediate	Generic affinity	Inferred
Cervidae	Capreolinae	*Blastoceras*	*dichotomus*	-	Marsh Deer	Intermediate	24% grasses	78
Cervidae	Capreolinae	*Capreolus*	*capreolus*	-	Western Roe Deer	Browser	<20% grasses	79
Cervidae	Capreolinae	*Hippocamelus*	*antisensis*	-	Peruvian Guemal	Intermediate	Generic affinity	Inferred
Cervidae	Capreolinae	*Mazama*	*americana*	-	Red Brocket	Browser	1% grasses	78
Cervidae	Capreolinae	*Mazama*	*gouazoubia*	-	Gray Brocket	Browser	Generic affinity	Inferred
Cervidae	Capreolinae	*Odocoileus*	*hemionus*	-	Mule Deer	Browser	Unknown	75
Cervidae	Capreolinae	*Odocoileus*	*virginianus*	-	White-Tailed Deer	Browser	9% grasses	78
Cervidae	Capreolinae	*Ozotoceras*	*bezoarticus*	-	Pampas Deer	Intermediate	Unknown	75
Cervidae	Capreolinae	*Pudu*	*puda*	-	Southern Pudu	Browser	3% grasses	78
Cervidae	Capreolinae	*Rangifer*	*tarandus*	-	Caribou	Intermediate	36% grasses	78
Cervidae	Cervinae	*Axis*	*axis*	-	Chital	Intermediate	70% grasses	78
Cervidae	Cervinae	*Cervus*	*axis*	*ceylonensis*	Axis Deer	Intermediate	Generic affinity	Inferred
Cervidae	Cervinae	*Cervus*	*duvauceli*	-	Barasingha	Intermediate	Mesodonty	76
Cervidae	Cervinae	*Cervus*	*elaphus*	-	Elk	Intermediate	20-80% grasses	79
Cervidae	Cervinae	*Cervus*	*eldii*	*eldii*	Eld's Deer	Intermediate	Unknown	75
Cervidae	Cervinae	*Cervus*	*kuhli*	-	Bawean Deer	Intermediate	Generic affinity	Inferred

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Principal Component	Eigenvalue	Weight percentage	Cumulative weight
1	**0.008744204**	**70.27120839**	**70.27120839**
2	**0.002308491**	**18.55176886**	**88.82297724**
3	**0.000498132**	**4.003146265**	**92.82612351**
4	**0.000433897**	**3.486933186**	**96.31305669**
5	0.000140905	1.132355925	97.44541262
6	8.84222E-05	0.710588766	98.15600138
7	4.80162E-05	0.38587358	98.54187496
8	3.66493E-05	0.294525103	98.83640007
9	3.17042E-05	0.254785269	99.09118534
10	2.84635E-05	0.228741376	99.31992671
11	1.69153E-05	0.135936947	99.45586366
12	1.40061E-05	0.112557612	99.56842127
13	9.52E-06	0.076493445	99.64491472
14	7.30E-06	0.058646932	99.70356165
15	6.53E-06	0.052500173	99.75606182
16	4.21E-06	0.033802483	99.7898643
17	3.92E-06	0.031478354	99.82134266
18	3.00E-06	0.024120104	99.84546276
19	2.54E-06	0.020388068	99.86585083
20	2.42E-06	0.019481692	99.88533252
21	2.20E-06	0.017685093	99.90301761
22	1.73E-06	0.013886896	99.91690451
23	1.62E-06	0.013004467	99.92990898
24	1.39E-06	0.011203534	99.94111251
25	9.85E-07	0.007913172	99.94902568
26	8.79E-07	0.007067246	99.95609293
27	7.57E-07	0.006080386	99.96217332
28	6.37E-07	0.005118647	99.96729196
29	6.13E-07	0.004927745	99.97221971
30	4.87E-07	0.003909996	99.9761297
31	3.95E-07	0.003173709	99.97930341
32	3.68E-07	0.0029577	99.98226111
33	2.73E-07	0.002193787	99.9844549
34	2.40E-07	0.001930324	99.98638522
35	1.97E-07	0.001584581	99.9879698
36	1.66E-07	0.001332252	99.98930206
37	1.57E-07	0.001258389	99.99056044
38	1.36E-07	0.001091492	99.99165194
39	1.26E-07	0.001009945	99.99266188
40	9.46E-08	0.000760303	99.99342219
41	8.58E-08	0.000689136	99.99411132
42	7.31E-08	0.000587238	99.99469856
43	6.60E-08	0.000530241	99.9952288
44	5.97E-08	0.000479493	99.99570829
45	5.59E-08	0.000449483	99.99615778
46	5.21E-08	0.000418662	99.99657644
47	4.36E-08	0.000350638	99.99692708
48	4.09E-08	0.000328789	99.99725587
49	3.64E-08	0.000292258	99.99754812
50	3.33E-08	0.000267282	99.99781541
51	3.27E-08	0.000263173	99.99807858

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Object	Group	PC-1	PC-2	PC-3	PC-4
Alces alces	Browser	0.145454275	0.015621	0.013565781	-0.046496309
Alces pulmatus	Browser	0.208680233	-0.011366524	0.008877719	-0.01333912
Ammodorcas clarkei	Browser	0.225894381	0.041229287	0.008656986	-0.023600831
Capreolus capreolus	Browser	-0.103939254	0.007084385	0.010658475	-0.061923283
Cephalophus dorsalis	Browser	-0.053598888	0.034522166	0.012326215	-0.089026237
Cephalophus harveyi	Browser	-0.006247012	0.061869374	0.024567406	-0.050736367
Cephalophus maxwelli	Browser	0.086915786	0.033052772	0.012767249	-0.0549472
Cephalophus natelensis	Browser	0.012564571	0.024147221	-0.033732709	-0.026708672
Cephalophus niger	Browser	-0.013981542	0.054525378	-0.013150764	-0.032842455
Cephalophus nigrifrons	Browser	-0.041466731	0.079054204	-0.001287868	-0.050137369
Cephalophus rufilatus	Browser	0.065699553	0.004281893	0.062167053	-0.064314754
Cephalophus silvicultor	Browser	-0.068118775	0.047441596	-0.00511401	-0.046983487
Cephalophus zebra	Browser	-0.113976127	0.067373108	0.018840127	-0.107802274
Elaphodus cephalophus	Browser	-0.014551888	0.083630139	-0.007465703	-0.045661126
Giraffa camelopardalis	Browser	0.135695201	0.00380996	0.025794466	-0.003491457
Litocranius walleri	Browser	0.098858942	0.077059098	0.016195154	-0.048828282
Madoqua cordeauxi	Browser	0.025785601	-0.050486124	-0.048495874	-0.095838342
Madoqua phillipsi	Browser	0.101734782	-0.047439902	-0.057051492	-0.076975429
Madoqua saltiana	Browser	-0.09826052	-0.052816096	-0.013686642	-0.056015304
Madoqua swaynei	Browser	0.149365751	0.062323968	-0.077477509	-0.064148731
Mazama americana	Browser	0.05254025	-0.028410543	-0.01537611	-0.040798542
Mazama gouazoubia	Browser	0.122532461	0.020987529	0.018492817	-0.063923003
Muntiacus crinifrons	Browser	0.001628589	0.057297723	0.006356642	-0.07699171
Muntiacus muntjak	Browser	0.009877039	0.036185309	-0.007108446	-0.037320206
Muntiacus reevesi	Browser	-0.031306032	0.046815311	-0.013621303	-0.054983611
Neotragus batesi	Browser	0.023165949	0.040266493	-0.006248303	-0.024822366
Neotragus moschatus	Browser	-0.108652149	0.038560968	-0.021836745	-0.032789545
Neotragus pygmaeus	Browser	-0.0454996	0.041921594	0.036061322	-0.045173206
Odocoileus hemionus	Browser	0.020308013	0.019168123	0.003916162	-0.089936721
Odocoileus virginianus	Browser	-0.00126213	0.001441239	-0.014397922	-0.041270959
Oreotragus oreotragus	Browser	-0.100084595	0.05265545	-0.022300798	-0.05918378
Pelea capreolus	Browser	-0.136503248	-0.004981306	0.004082033	-0.040892893
Pudu puda	Browser	-0.090855714	0.006114476	0.001953238	-0.017204165
Raphicerus campestris	Browser	0.059281134	0.022940536	-0.031084891	-0.020590339
Rhynchotragus domorensis	Browser	0.142956174	-0.082654523	-0.046230473	-0.06573981
Rhynchotragus kirkii	Browser	0.037570768	-0.10097806	0.010424078	-0.057094207
Rhyncotragus guentheri	Browser	0.036477118	-0.07517353	0.035073131	-0.081654623
Tragelaphus buxtoni	Browser	-0.087414461	0.021363821	-0.005979936	-0.071551522
Tragelaphus eurycerus	Browser	-0.140793742	0.049399112	-0.020457587	-0.014190112
Tragelaphus imberbis	Browser	-0.034701419	-0.009433553	-0.004416701	-0.042321426
Tragelaphus scriptus	Browser	-0.040943975	0.015610834	-0.025280239	-0.00661339
Tragelaphus strepticeros	Browser	-0.029531932	0.015559751	0.008978674	-0.064384459
Tragulus javanicus	Browser	-0.11821129	0.079199663	-0.017391446	-0.047505796
Tragulus kanchil	Browser	-0.143511683	0.112666705	-0.004730488	-0.050040736
Tragulus napu	Browser	-0.057967138	0.070638312	-0.020733404	-0.059400314
Addax nasomaculatus	Grazer	0.016879504	-0.016675734	-0.015102416	-0.067243153
Alcelaphus buselaphus	Grazer	-0.112619795	-0.022754223	-0.006537528	-0.052680022
Beatragus hunteri	Grazer	-0.143204854	0.001164212	-0.023103802	-0.046950791
Connochaetes gnou	Grazer	-0.114919761	-0.121170035	0.005968644	-0.047100595
Connochaetes taurinus	Grazer	-0.24532758	-0.057737442	0.00939017	-0.020851506
Damaliscus albifrons	Grazer	-0.083456558	-0.068615892	0.020768153	-0.034307823
Damaliscus dorcas	Grazer	-0.054280476	-0.041839954	-0.003530996	-0.050508413
Damaliscus korrigum	Grazer	-0.096379985	-0.017812656	-0.011417381	-0.059657253
Damaliscus liechtensteinii	Grazer	-0.008402857	-0.025137662	-0.016126486	-0.036003165
Damaliscus lunatus	Grazer	-0.088051244	-0.015703577	-0.032360953	-0.044005587
Damaliscus pygargus	Grazer	-0.053107117	-0.033838922	0.001556381	-0.061565991
Elaphurus davidianus	Grazer	0.009837772	0.002252316	-0.011942385	-0.049946122
Hippotragus equinus	Grazer	-0.038413857	-0.023256843	-0.013572069	-0.02866432
Hippotragus niger	Grazer	-0.060788344	-0.034540125	-0.003088193	-0.021244428
Kobus defassa	Grazer	-0.083568589	-0.000959899	0.002773324	-0.061373631
Kobus ellipsiprymnus	Grazer	-0.056893072	-0.018136384	-0.0162717	-0.030482489
Kobus kob	Grazer	0.006612936	-0.043474261	-0.020899782	-0.052035652
Kobus leche	Grazer	-0.132037077	-0.024183085	0.000583302	-0.044845453
Kobus megaceros	Grazer	-0.064007775	-0.008846466	-0.042657559	-0.046014138
Kobus vardonii	Grazer	-0.049911369	-0.050050634	0.022286528	-0.033481497
Oryx beisa	Grazer	0.073316659	-0.043784623	-0.014512298	-0.06470243
Oryx gazella	Grazer	-0.009241278	-0.059445577	0.01275811	-0.0288494
Oryx leucoryx	Grazer	-0.203808498	0.028229774	-0.011354211	-0.040584747
Redunca redunca	Grazer	-0.08255385	-0.054204473	-0.015456252	-0.052017216
Tetracerus quadricornis	Grazer	0.083553349	0.014989391	-0.006848081	-0.020545831
Aepyceros melampus	Unknown	0.10915647	0.029872523	-0.000500701	-0.02601028
Antidorcas marsupialis	Unknown	0.197436012	0.067694475	0.009876004	-0.071379907
Antilocapra americana	Unknown	0.00625664	0.067986715	-0.033075229	-0.061050249
Antilope cervicapra	Unknown	0.059834303	-0.033081895	-0.037002499	-0.064085992
Axis axis	Unknown	-0.058638706	0.017252124	-0.003052959	-0.065040948
Blastoceras bezoarticus	Unknown	0.049090604	-0.053182643	0.020274755	-0.080208002
Blastoceras dichotomus	Unknown	-0.01103972	-0.015316786	-0.008025706	-0.051369093
Boselaphus tragocamelus	Unknown	-0.036525519	-0.031077584	0.003716336	-0.03011864
Cervus axis	Unknown	-0.10183954	0.022663033	-0.030973305	-0.058671658
Cervus duvauceli	Unknown	-0.076898341	0.069813188	0.012067326	-0.101985441
Cervus eldii	Unknown	0.003534505	-0.037227395	0.016588359	-0.034612717
Cervus elaphus	Unknown	-0.106593411	0.016358342	-0.020034668	-0.076267237
Cervus kuhli	Unknown	-0.059475904	-0.037666361	-0.000314599	-0.044219932
Cervus nippon	Unknown	-0.066148036	-0.008322469	-0.005278191	-0.058510053
Cervus schomburgki	Unknown	-0.020925257	0.033888994	-0.008025976	-0.078520522
Cervus timorensis	Unknown	-0.063426451	0.032988004	0.013694422	-0.070167468
Cervus unicolor	Unknown	0.007449944	-0.009801992	-0.009060498	-0.048978894
Dama dama	Unknown	-0.116504212	0.014466294	-0.018270678	-0.071586928
Dorcatragus megalotis	Unknown	0.281497814	0.036541161	0.024368369	-0.038299639
Eudorcas thomsoni	Unknown	0.204736702	0.017138503	0.015210713	-0.092663727
Gazella spekei	Unknown	-0.151480371	0.008664012	-0.045044173	-0.035939025
Gazella bennettii	Unknown	0.023107498	0.00409612	0.010053607	-0.103464299
Gazella cuvieri	Unknown	-0.063158699	-0.018983986	-0.009249916	-0.075378732
Gazella dama	Unknown	0.138361467	0.029476414	-0.011564786	-0.064898059
Gazella dorcas	Unknown	0.034165948	-0.043552979	-0.006442683	-0.099655566
Gazella gazella	Unknown	0.123344334	0.073442516	0.042690351	-0.116095208
Gazella leptoceros	Unknown	0.046906749	0.067269737	-0.015849462	-0.05901743
Gazella rufifrons	Unknown	0.06989796	-0.047645131	-0.016280505	-0.069042833
Gazella saudiya	Unknown	0.053911135	0.024784884	-0.030771658	-0.04774911
Gazella soemmeringi	Unknown	0.091710631	0.032358482	-0.008159245	-0.098693264
Gazella subgutturosa	Unknown	0.090153635	-0.01423704	-0.015566343	-0.054700341
Hippocamelus antisensis	Unknown	-0.014698971	-0.00979739	0.001617604	-0.057400485
Hydropodus inermis	Unknown	-0.192159705	0.124973075	-0.00632311	-0.053701285
Moschus moschiferous	Unknown	-0.041170242	0.048257035	-0.050335732	-0.019275178
Nanger granti	Unknown	0.08610612	0.023809306	-0.019426193	-0.066744901

Supplementary Information 2, tabs 1, 2, 3, and 4

Object	Group	CV-1	CV-2	CV-3	CV-4
Alces alces	Browser	-0.07777	0.010704	-0.08185	-0.04934
Alces pulmatus	Browser	-0.05484	0.004861	-0.12225	-0.11904
Ammodorcas clarkei	Browser	-0.10554	0.002548	-0.09795	-0.08958
Capreolus capreolus	Browser	-0.01331	0.014082	0.037389	0.093841
Cephalophus dorsalis	Browser	-0.06245	0.014196	0.019733	0.095663
Cephalophus harveyi	Browser	-0.07868	0.023518	0.03224	0.071873
Cephalophus maxwelli	Browser	-0.08025	0.010774	-0.04194	-0.00076
Cephalophus natelensis	Browser	-0.02849	-0.03428	-0.00729	0.014252
Cephalophus niger	Browser	-0.05301	-0.0141	0.030367	0.05618
Cephalophus nigrifrons	Browser	-0.07665	-0.00215	0.057991	0.098105
Cephalophus rufilatus	Browser	-0.06844	0.061854	-0.04464	0.006048
Cephalophus silvicultor	Browser	-0.0426	-0.00428	0.049977	0.090307
Cephalophus zebra	Browser	-0.08351	0.021271	0.069016	0.161511
Elaphodus cephalophus	Browser	-0.0835	-0.0092	0.047504	0.08256
Giraffa camelopardalis	Browser	-0.04615	0.022636	-0.06517	-0.06848
Litocranius walleri	Browser	-0.1151	0.012184	-0.0136	0.019397
Madoqua cordeauxi	Browser	-0.00707	-0.04509	-0.09871	-0.01446
Madoqua phillipsi	Browser	-0.01745	-0.05587	-0.13097	-0.06592
Madoqua saltiana	Browser	0.040325	-0.0083	-0.0112	0.043716
Madoqua swaynei	Browser	-0.10379	-0.08165	-0.07684	-0.03032
Mazama americana	Browser	-0.00971	-0.01462	-0.06789	-0.03345
Mazama gouazoubia	Browser	-0.08622	0.016326	-0.07186	-0.02395
Muntiacus crinifrons	Browser	-0.08691	0.005889	0.010352	0.072617
Muntiacus muntjak	Browser	-0.04874	-0.00784	0.004069	0.033605
Muntiacus reevesi	Browser	-0.05404	-0.01342	0.024992	0.070813
Neotragus batesi	Browser	-0.049	-0.0077	0.005174	0.023276
Neotragus moschatus	Browser	-0.01384	-0.02006	0.067319	0.098027
Neotragus pygmaeus	Browser	-0.05258	0.036495	0.043449	0.080839
Odocoileus hemionus	Browser	-0.06846	0.004708	-0.03256	0.042096
Odocoileus virginianus	Browser	-0.01927	-0.01351	-0.01801	0.017394
Oreotragus oreotragus	Browser	-0.04082	-0.02065	0.062098	0.114174
Pelea capreolus	Browser	0.017144	0.008233	0.05313	0.093791
Pudu puda	Browser	0.009536	0.004154	0.045991	0.064022
Raphicerus campestris	Browser	-0.03716	-0.03278	-0.02988	-0.01546
Rhynchotragus domorensis	Browser	0.002573	-0.04495	-0.17118	-0.11568
Rhynchotragus kirkii	Browser	0.036148	0.014505	-0.113	-0.06057
Rhyncotragus guentheri	Browser	-0.00211	0.038739	-0.09869	-0.02717
Tragelaphus buxtoni	Browser	-0.03004	-0.00322	0.031447	0.094947
Tragelaphus eurycerus	Browser	-0.00435	-0.01875	0.09991	0.115479
Tragelaphus imberbis	Browser	-0.00488	-0.00236	-0.00638	0.031703
Tragelaphus scriptus	Browser	0.000824	-0.02475	0.024867	0.031805
Tragelaphus streptisceros	Browser	-0.04029	0.010467	0.002664	0.057711
Tragulus javanicus	Browser	-0.05165	-0.01657	0.096441	0.13777
Tragulus kanchil	Browser	-0.07521	-0.00452	0.13543	0.177892
Tragulus napu	Browser	-0.06628	-0.02069	0.052878	0.102388
Addax nasomaculatus	Grazer	-0.02348	-0.01339	-0.05122	0.006565
Alcelaphus buselaphus	Grazer	0.020883	-0.00201	0.02076	0.071651
Beatragus hunteri	Grazer	0.017077	-0.01886	0.0529	0.099169
Connochaetes gnou	Grazer	0.098021	0.014021	-0.04351	0.007876
Connochaetes taurinus	Grazer	0.095959	0.017489	0.082295	0.113162
Damaliscus albifrons	Grazer	0.052369	0.025889	-0.01432	0.021721
Damaliscus dorcas	Grazer	0.020894	0.000331	-0.0223	0.025325

Groups	Browser	Grazer	Total Correct	Group Totals	Percent Correct
Browser	34	11	34	45	**75.56**
Grazer	4	21	21	25	**84.00**
Total Correct	34	21	55	70	**78.57**
Total Estmated	38	32	70		
Percent Estimated Correctly	**89.47**	**65.63**	**78.57**		

Groups	Browser	Grazer	Total Correct	Group Totals	Percent Correct
Browser	32	13	32	45	**71.11**
Grazer	4	21	21	25	**84.00**
Total Correct	32	21	53	70	**75.71**
Total Estmated	36	34	70		
Percent Estimated Correctly	**88.89**	**61.76**	**75.71**		

Object	Group	Browser	Grazer
Alces alces	Browser	**0.035**	0.096
Alces pulmatus	Browser	**0.012**	0.073
Ammodorcas clarkei	Browser	**0.063**	0.124
Capreolus capreolus	Browser	**0.030**	0.031
Cephalophus dorsalis	Browser	**0.019**	0.081
Cephalophus harveyi	Browser	**0.036**	0.097
Cephalophus maxwelli	Browser	**0.037**	0.098
Cephalophus natelensis	Browser	**0.014**	0.047
Cephalophus niger	Browser	**0.010**	0.071
Cephalophus nigrifrons	Browser	**0.034**	0.095
Cephalophus rufilatus	Browser	**0.025**	0.087
Cephalophus silvicultor	Browser	**0.000**	0.061
Cephalophus zebra	Browser	**0.041**	0.102
Elaphodus cephalophus	Browser	**0.041**	0.102
Giraffa camelopardalis	Browser	**0.003**	0.064
Litocranius walleri	Browser	**0.072**	0.133
Madoqua cordeauxi	Browser	0.036	**0.025**
Madoqua phillipsi	Browser	**0.026**	0.036
Madoqua saltiana	Browser	0.083	**0.022**
Madoqua swaynei	Browser	**0.061**	0.122
Mazama americana	Browser	0.033	**0.028**
Mazama gouazoubia	Browser	**0.043**	0.104
Muntiacus crinifrons	Browser	**0.044**	0.105
Muntiacus muntjak	Browser	**0.006**	0.067
Muntiacus reevesi	Browser	**0.011**	0.072
Neotragus batesi	Browser	**0.006**	0.067
Neotragus moschatus	Browser	**0.029**	0.032
Neotragus pygmaeus	Browser	**0.010**	0.071
Odocoileus hemionus	Browser	**0.025**	0.087
Odocoileus virginianus	Browser	**0.024**	0.037
Oreotragus oreotragus	Browser	**0.002**	0.059
Pelea capreolus	Browser	0.060	**0.001**
Pudu puda	Browser	0.053	**0.009**
Raphicerus campestris	Browser	**0.006**	0.055
Rhynchotragus domorensis	Browser	0.046	**0.016**
Rhynchotragus kirkii	Browser	0.079	**0.018**
Rhyncotragus guentheri	Browser	0.041	**0.020**
Tragelaphus buxtoni	Browser	**0.013**	0.048
Tragelaphus eurycerus	Browser	0.039	**0.022**
Tragelaphus imberbis	Browser	0.038	**0.023**
Tragelaphus scriptus	Browser	0.044	**0.017**
Tragelaphus streptisceros	Browser	**0.003**	0.058
Tragulus javanicus	Browser	**0.009**	0.070
Tragulus kanchil	Browser	**0.032**	0.093
Tragulus napu	Browser	**0.023**	0.084
Addax nasomaculatus	Grazer	**0.019**	0.042
Alcelaphus buselaphus	Grazer	0.064	**0.003**
Beatragus hunteri	Grazer	0.060	**0.001**
Connochaetes gnou	Grazer	0.141	**0.080**
Connochaetes taurinus	Grazer	0.139	**0.078**
Damaliscus albifrons	Grazer	0.095	**0.034**
Damaliscus dorcas	Grazer	0.064	**0.003**
Damaliscus korrigum	Grazer	0.053	**0.008**
Damaliscus liechtensteinii	Grazer	0.049	**0.012**
Damaliscus lunatus	Grazer	0.062	**0.001**
Damaliscus pygargus	Grazer	0.050	**0.011**
Elaphurus davidianus	Grazer	**0.015**	0.046
Hippotragus equinus	Grazer	0.059	**0.002**
Hippotragus niger	Grazer	0.075	**0.014**
Kobus defassa	Grazer	0.033	**0.028**
Kobus ellipsiprymnus	Grazer	0.060	**0.002**
Kobus kob	Grazer	0.052	**0.009**
Kobus leche	Grazer	0.073	**0.011**
Kobus megaceros	Grazer	0.052	**0.009**
Kobus vardonii	Grazer	0.072	**0.011**
Oryx beisa	Grazer	**0.027**	0.034
Oryx gazella	Grazer	0.073	**0.012**
Oryx leucoryx	Grazer	0.056	**0.006**
Redunca redunca	Grazer	0.083	**0.022**
Tetracerus quadricornis	Grazer	**0.000**	0.061
Aepyceros melampus	Unknown	**0.022**	0.083
Antidorcas marsupialis	Unknown	**0.101**	0.162
Antilocapra americana	Unknown	**0.036**	0.097
Antilope cervicapra	Unknown	**0.028**	0.033
Axis axis	Unknown	**0.011**	0.050
Blastoceras bezoarticus	Unknown	**0.025**	0.037
Blastoceras dichotomus	Unknown	0.033	**0.029**
Boselaphus tragocamelus	Unknown	0.060	**0.001**
Cervus axis	Unknown	**0.028**	0.033
Cervus duvauceli	Unknown	**0.048**	0.109
Cervus eldii	Unknown	0.049	**0.012**
Cervus elaphus	Unknown	**0.023**	0.039
Cervus kuhli	Unknown	0.065	**0.003**
Cervus nippon	Unknown	0.037	**0.024**
Cervus schomburgki	Unknown	**0.017**	0.079
Cervus timorensis	Unknown	**0.006**	0.067
Cervus unicolor	Unknown	**0.025**	0.036
Dama dama	Unknown	**0.029**	0.032
Dorcatragus megalotis	Unknown	**0.085**	0.146
Eudorcas thomsoni	Unknown	**0.076**	0.137
Gazella spekei	Unknown	0.067	**0.006**
Gazella bennettii	Unknown	**0.023**	0.084
Gazella cuvieri	Unknown	0.037	**0.024**
Gazella dama	Unknown	**0.048**	0.109
Gazella dorcas	Unknown	**0.017**	0.044
Gazella gazella	Unknown	**0.117**	0.178
Gazella leptoceros	Unknown	**0.049**	0.110
Gazella rufifrons	Unknown	**0.029**	0.032
Gazella saudiya	Unknown	**0.009**	0.070
Gazella soemmeringi	Unknown	**0.056**	0.117
Gazella subgutturosa	Unknown	**0.005**	0.056
Hippocamelus antisensis	Unknown	**0.024**	0.037
Hydropodus inermis	Unknown	**0.031**	0.092
Moschus moschiferous	Unknown	**0.017**	0.044
Nanger granti	Unknown	**0.029**	0.090
Ourebia ourebi	Unknown	**0.043**	0.104
Ozotoceras bezoarticus	Unknown	0.036	**0.025**
Procapra gutturosa	Unknown	0.043	**0.018**
Procapra picticaudata	Unknown	**0.005**	0.066
Procapra przewalskii	Unknown	**0.004**	0.058
Pseudois nayaur	Unknown	**0.073**	0.135
Rangifer tarandus	Unknown	**0.066**	0.127
Raphicerus melanotis	Unknown	**0.037**	0.098
Raphicerus sharpei	Unknown	**0.019**	0.080
Redunca fulvurofula	Unknown	0.031	**0.030**
Taurotragus oryx	Unknown	0.055	**0.006**
Tragelaphus angasi	Unknown	**0.024**	0.037
Tragelaphus spekii	Unknown	0.037	**0.024**

Supplementary Information 3, tabs 1 and 2

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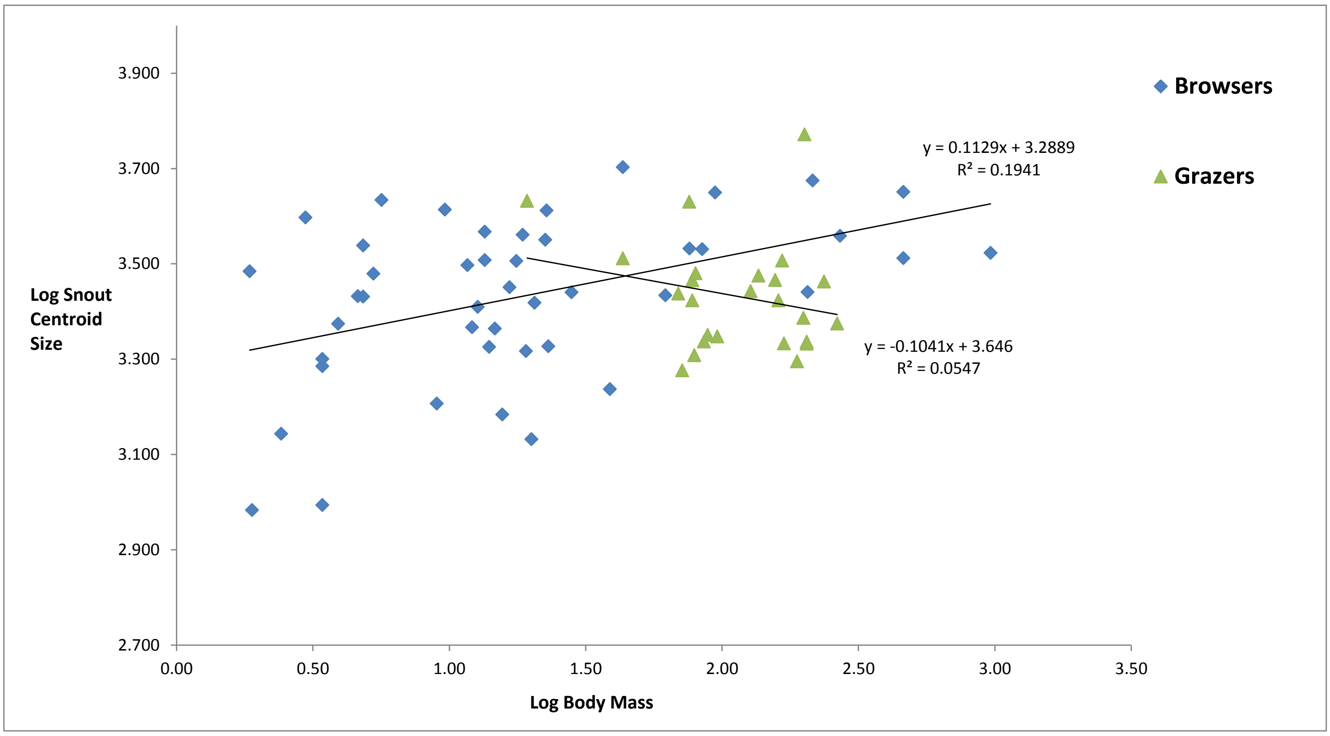
Family	Taxon	Ecology	Adult body mass (kg)	Log Body Mass	Snout Centroid Size	Log Snout Centroid Size
Bovidae	*Ammodorcas clarkei*	Browser	28.05	1.45	2756.169	3.440
Bovidae	*Litocranius walleri*	Browser	38.80	1.59	1726.607	3.237
Bovidae	*Madoqua cordeauxi*	Browser	3.42	0.53	1928.744	3.285
Bovidae	*Madoqua phillipsi*	Browser	2.42	0.38	1392.285	3.144
Bovidae	*Madoqua saltiana*	Browser	3.42	0.53	986.410	2.994
Bovidae	*Madoqua swaynei*	Browser	3.42	0.53	1997.255	3.300
Bovidae	*Neotragus batesi*	Browser	2.97	0.47	3954.951	3.597
Bovidae	*Neotragus moschatus*	Browser	5.64	0.75	4303.161	3.634
Bovidae	*Neotragus pygmaeus*	Browser	3.91	0.59	2367.418	3.374
Bovidae	*Oreotragus oreotragus*	Browser	13.49	1.13	3218.679	3.508
Bovidae	*Raphicerus campestris*	Browser	11.66	1.07	3143.399	3.497
Bovidae	*Rhynchotragus damarensis*	Browser	4.83	0.68	3454.148	3.538
Bovidae	*Rhynchotragus guentheri*	Browser	4.62	0.66	2704.035	3.432
Bovidae	*Rhynchotragus kirkii*	Browser	4.83	0.68	2698.891	3.431
Bovidae	*Tragelaphus buxtoni*	Browser	215.00	2.33	4727.972	3.675
Bovidae	*Tragelaphus eurycerus*	Browser	271.00	2.43	3619.837	3.559
Bovidae	*Tragelaphus imberbis*	Browser	94.32	1.97	4461.278	3.649
Bovidae	*Tragelaphus scriptus*	Browser	43.25	1.64	5045.136	3.703
Bovidae	*Tragelaphus streptisceros*	Browser	206.06	2.31	2759.638	3.441
Bovidae	*Cephalophus dorsalis*	Browser	20.00	1.30	1354.819	3.132
Bovidae	*Cephalophus harveyi*	Browser	14.00	1.15	2115.711	3.325
Bovidae	*Cephalophus maxwelli*	Browser	9.00	0.95	1610.351	3.207
Bovidae	*Cephalophus natelensis*	Browser	12.72	1.10	2568.019	3.410
Bovidae	*Cephalophus niger*	Browser	19.09	1.28	2074.010	3.317
Bovidae	*Cephalophus nigrifrons*	Browser	14.68	1.17	2314.119	3.364
Bovidae	*Cephalophus rufilatus*	Browser	12.11	1.08	2328.915	3.367
Bovidae	*Cephalophus silvicultor*	Browser	62.01	1.79	2715.617	3.434
Bovidae	*Cephalophus zebra*	Browser	15.65	1.19	1527.410	3.184
Bovidae	*Pelea capreolus*	Browser	22.73	1.36	4093.561	3.612
Cervidae	*Alces alces*	Browser	461.90	2.66	4478.341	3.651
Cervidae	*Alces palmatus*	Browser	461.90	2.66	3248.610	3.512
Cervidae	*Capreolus capreolus*	Browser	22.50	1.35	3552.707	3.551
Cervidae	*Mazama americana*	Browser	20.55	1.31	2621.214	3.419
Cervidae	*Mazama gouazoubia*	Browser	16.63	1.22	2824.186	3.451
Cervidae	*Odocoileus hemionus*	Browser	84.56	1.93	3395.717	3.531
Cervidae	*Odocoileus virginianus*	Browser	75.90	1.88	3405.820	3.532
Cervidae	*Pudu puda*	Browser	9.64	0.98	4108.340	3.614
Cervidae	*Elaphodus cephalophus*	Browser	23.09	1.36	2122.659	3.327
Cervidae	*Muntiacus crinifrons*	Browser	18.59	1.27	3638.542	3.561
Cervidae	*Muntiacus muntjak*	Browser	17.61	1.25	3204.666	3.506
Cervidae	*Muntiacus reevesi*	Browser	13.50	1.13	3695.277	3.568
Giraffidae	*Giraffa camelopardalis*	Browser	964.65	2.98	3334.062	3.523
Tragulidae	*Tragulus javanicus*	Browser	1.89	0.28	961.985	2.983
Tragulidae	*Tragulus kanchil*	Browser	1.85	0.27	3049.187	3.484
Tragulidae	*Tragulus napu*	Browser	5.27	0.72	3016.284	3.479
Bovidae	*Cephalophus monticola*	Frugivore	4.00	0.60	1884.351	3.275
Bovidae	*Sylvicapra grimmia*	Frugivore	15.64	1.19	3650.326	3.562
Bovidae	*Redunca arundinum*	Frugivore	58.06	1.76	3752.398	3.574
Bovidae	*Alcelaphus buselaphus*	Grazer	160.94	2.21	2650.229	3.423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Grazers
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Log Snout Centroid Size
Log Body Mass
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3.700
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1.50
2.00
2.50
3.00
3.50

Family	Taxon	Ecology	Adult body mass (kg)	Log Body Mass	Snout Centroid Size	Log Snout Centroid Size
Bovidae	***Aepyceros melampus***	Browser	52.59	1.72	6448.624	3.809
Cervidae	*Alces alces*	Browser	461.90	2.66	4478.341	3.651
Cervidae	*Alces palmatus*	Browser	461.90	2.66	3248.610	3.512
Bovidae	*Ammodorcas clarkei*	Browser	28.05	1.45	2756.169	3.440
Bovidae	***Antidorcas marsupialis***	Browser	33.57	1.53	3428.877	3.535
Antilocapridae	***Antilocapra americana***	Browser	47.45	1.68	3657.086	3.563
Bovidae	***Antilope cervicapra***	Browser	36.30	1.56	1109.046	3.045
Cervidae	***Axis axis***	Browser	69.50	1.84	1767.446	3.247
Cervidae	***Blastoceras bezoarticus***	Browser	112.52	2.05	2870.992	3.458
Cervidae	*Capreolus capreolus*	Browser	22.50	1.35	3552.707	3.551
Bovidae	*Cephalophus dorsalis*	Browser	20.00	1.30	1354.819	3.132
Bovidae	*Cephalophus harveyi*	Browser	14.00	1.15	2115.711	3.325
Bovidae	*Cephalophus maxwelli*	Browser	9.00	0.95	1610.351	3.207
Bovidae	*Cephalophus natelensis*	Browser	12.72	1.10	2568.019	3.410
Bovidae	*Cephalophus niger*	Browser	19.09	1.28	2074.010	3.317
Bovidae	*Cephalophus nigrifrons*	Browser	14.68	1.17	2314.119	3.364
Bovidae	*Cephalophus rufilatus*	Browser	12.11	1.08	2328.915	3.367
Bovidae	*Cephalophus silvicultor*	Browser	62.01	1.79	2715.617	3.434
Bovidae	*Cephalophus zebra*	Browser	15.65	1.19	1527.410	3.184
Cervidae	***Cervus axis***	Browser	55.00	1.74	2052.563	3.312
Cervidae	***Cervus duvauceli***	Browser	150.00	2.18	2024.273	3.306
Cervidae	***Cervus elaphus***	Browser	240.87	2.38	2473.069	3.393
Cervidae	***Cervus schomburgki***	Browser	107.63	2.03	2984.295	3.475
Cervidae	***Cervus timorensis***	Browser	66.38	1.82	2339.119	3.369
Cervidae	***Cervus unicolor***	Browser	177.52	2.25	2991.497	3.476
Cervidae	***Dama dama***	Browser	57.22	1.76	5936.135	3.774
Bovidae	***Dorcatragus megalotis***	Browser	10.92	1.04	4451.143	3.648
Cervidae	*Elaphodus cephalophus*	Browser	23.09	1.36	2122.659	3.327
Bovidae	***Eudorcas thomsoni***	Browser	22.91	1.36	929.841	2.968
Bovidae	***Gazella bennettii***	Browser	18.92	1.28	2061.958	3.314
Bovidae	***Gazella dama***	Browser	71.42	1.85	1902.351	3.279
Bovidae	***Gazella dorcas***	Browser	15.64	1.19	1500.511	3.176
Bovidae	***Gazella gazella***	Browser	21.31	1.33	2531.851	3.403
Bovidae	***Gazella leptoceros***	Browser	24.65	1.39	2909.337	3.464
Bovidae	***Gazella rufifrons***	Browser	27.00	1.43	1783.645	3.251
Bovidae	***Gazella saudiya***	Browser	16.00	1.20	2939.651	3.468
Bovidae	***Gazella soemmeringi***	Browser	41.58	1.62	1346.442	3.129
Bovidae	***Gazella subgutturosa***	Browser	26.98	1.43	1892.006	3.277
Giraffidae	*Giraffa camelopardalis*	Browser	964.65	2.98	3334.062	3.523
Cervidae	***Hippocamelus antisensis***	Browser	68.60	1.84	2810.277	3.449
Cervidae	***Hydropodus inermis***	Browser	12.76	1.11	1292.537	3.111
Bovidae	*Litocranius walleri*	Browser	38.80	1.59	1726.607	3.237
Bovidae	*Madoqua cordeauxi*	Browser	3.42	0.53	1928.744	3.285
Bovidae	*Madoqua phillipsi*	Browser	2.42	0.38	1392.285	3.144
Bovidae	*Madoqua saltiana*	Browser	3.42	0.53	986.410	2.994
Bovidae	*Madoqua swaynei*	Browser	3.42	0.53	1997.255	3.300
Cervidae	*Mazama americana*	Browser	20.55	1.31	2621.214	3.419
Cervidae	*Mazama gouazoubia*	Browser	16.63	1.22	2824.186	3.451
Moschidae	***Moschus moschiferous***	Browser	13.32	1.12	4546.366	3.658

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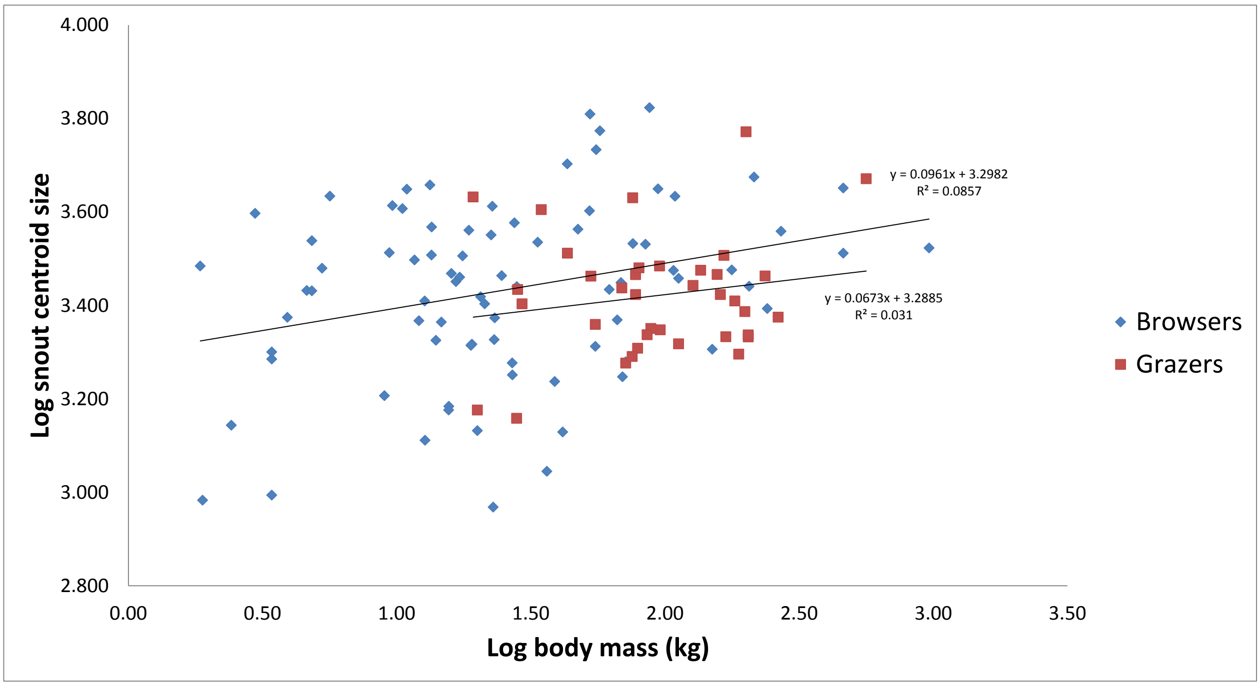

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