THE ROYAL SOCIETY

doi 10.1098/rspb.2001.1619

Relationships between oral morphology and feeding style in the Ungulata: a phylogenetically controlled evaluation

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In ungulates it is argued that specialization in the consumption of a particular type of food (feeding style) is reflected in morphological adaptations of the organs involved in the selection, processing and digestion of food. We analysed the differences in size and morphology of some oral traits that have been functionally related to food-selection ability (muzzle width, incisor-arcade shape, incisor shape), prehension of food (incisor protrusion), food comminution (molar occlusal surface area, hypsodonty (high-crowned molars)) and intake rate (incisor breadth) between ungulate species with different feeding styles (browser, mixed feeder, grazer). Grazers were characterized by large-body-size species. After controlling only for body mass, we found that grazers had wider muzzles and incisors, more-protruding incisors and more-bulky and higher-crowned molars than did mixed feeders and browsers. When the analyses took into account both body mass and phylogeny, only body mass and two out of the three hypsodonty indexes used remained significantly different between feeding styles. Browsers were smaller, on average, than mixed feeders and grazers, whilst grazers and mixed feeders did not differ in size. Also, browsers had shorter and less-bulky molars than did mixed feeders and grazers; the latter two feeding styles did not differ from each other in any of the hypsodonty indexes. We conclude that the adaptation to different dietary types in most of the oral traits studied is subsumed by the effects of body mass and the sharing of common ancestors. We hypothesize that differences in the ability to exploit different food resources primarily result from differences in body mass between species, and also discuss why hypsodonty characterizes feeding styles.

Keywords: allometry; body mass; comparative method; food selection; intake; browser–grazer

1. INTRODUCTION

The feeding-style classification of ungulates was originally defined by Van Zyl (1965), although Hofmann (1973) was the first to describe in detail the morphological differences in rumen and omasum structures of African ruminants with different diets. The classification divides the Ungulata into three main groups on the basis of the main type of herbage in their diets: browsing species, grazing species and species that both browse and graze, namely mixed feeders.

The intake and selection of food by artiodactyl ruminants have been closely linked with the size and shape of the animal's mouth: incisor breadth (Gordon *et al.* 1996), incisor-arcade shape (Gordon & Illius 1988), muzzle width (Bell 1969) and the width of the first incisor (Boué 1970; Janis & Ehrhardt 1988). Species that feed predominantly on grasses are hypothesized to have flatter incisor arcades than do browsing species of similar body mass (Gordon & Illius 1988), and also to have wider mouths that are able to grasp a greater quantity of vegetation, at the expense of the selection of small items of high-quality food. Likewise, the occlusal surface area of the post-canine tooth row has been related to the quantity, abrasiveness and mechanical resistance to comminution of the ingested food (Pérez-Barbería & Gordon 1998*a*), with grazers having a larger occlusal surface area to grind coarse foods, while browsers have a smaller and narrower post-canine tooth row but more-prominent dental crests adapted to puncturing the cell walls of browsed material (Fortelius 1985; Janis 1988; Solounias *et al.* 1994).

Although differences in oral morphology between feeding styles have been supported by both qualitative and quantitative observations (Bell 1969; Kay 1978; Gordon & Illius 1988; Hofmann 1988; Janis 1988; Janis & Ehrhardt 1988), none of these studies have considered the effect of the phylogenetic relationships between ungulate species on these oral-morphology traits. Due to the hierarchical structure of the phylogeny, species cannot be considered as independent entities (Felsenstein 1985; Harvey & Pagel 1991) and thus the use of classical statistical analyses inflates the degrees of freedom and distributes the total variance inappropriately, overestimating the power of the analyses. As such, previous approaches to the study of mouth morphology and feeding style may confound the effects of sharing common ancestors and the adaptive response.

It has been suggested that oral morphology within feeding style varies in relation to body mass (Gordon & Illius 1988). This is expected because oral morphology is understood to be a trade-off between intake rate and diet selection: smaller species are more selective than large species, regardless of their feeding style.

The purpose of this study was to test, first, whether there are differences between ungulate species with different feeding styles in some oral-morphology traits that have been suggested to confer advantages in food-intake rate, selection ability and processing, and, second,

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Received 20 December 2000 *Accepted* 9 February 2001

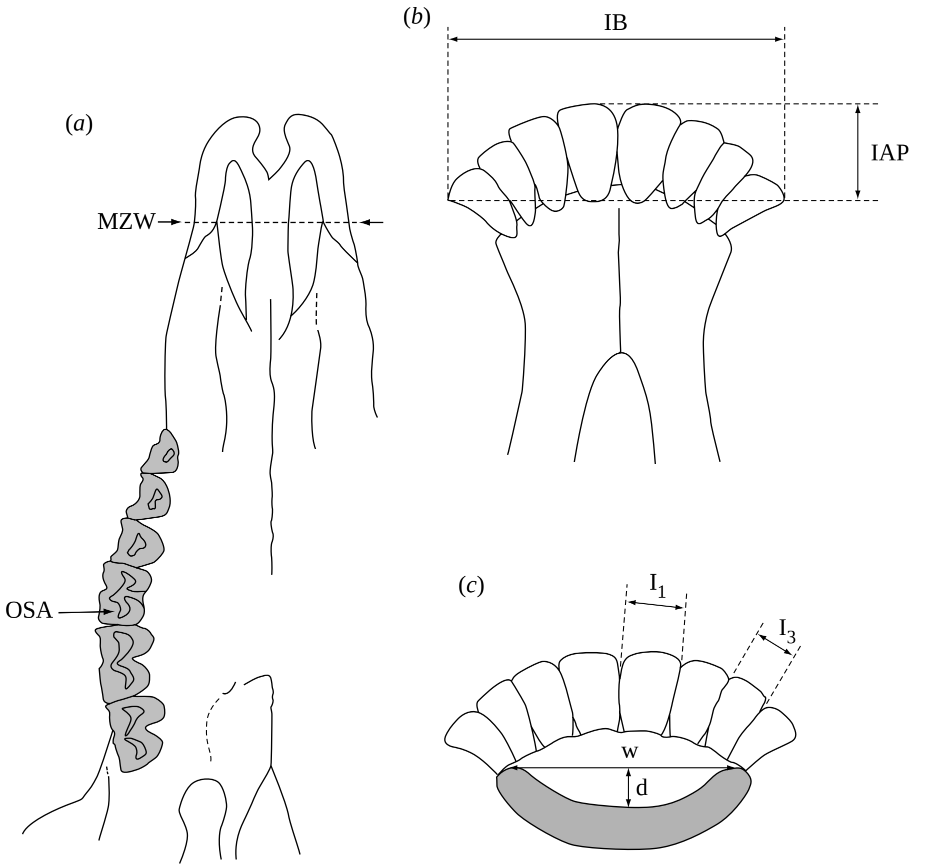

Figure 1. Diagrams showing the morphological oral traits used in this study. (*a*) Skull in occlusal view; MZW, muzzle width, measured at the junction between the maxillary and premaxillary bones; OSA, premolar and molar occlusal surface area, obtained by multiplying the length (mesiodistal diameter) by the width (buccolingual diameter) of each post-canine tooth of one ramus of the mandible and then summing the values. (*b*) Incisor arcade in occlusal view; IB, incisor breadth, measured as the distance between the outermost points of the incisiform canines of each ramus; IAP, protrusion of the incisor arcade, measured as the perpendicular distance to the front of the incisor arcade from a line between both incisiform canines divided by the incisor breadth. (*c*) transverse section of the mandibular symphysis across the canines, viewed from caudal to rostral direction; incisor shape, calculated as the first-incisor (I_1) width divided by the third-incisor (I_3) width; incisor protrusion, measured as the width across the mandibular symphysis (w) at the base of the canine tooth divided by the depth of the mandibular symphysis (d), being the depth of mandibular symphysis, the gap between a straight line across the points of insertion of the canines and the mandible on the midline.

how mouth morphology relates to body mass when phylogeny is taken into account.

We hypothesized that browsing species would exhibit an oral morphology that enables them to increase food selection (i.e. narrower incisor breadths and muzzles, more-protrusive incisor arcades, wider first incisors in relation to the other incisors and more-upright incisors) compared with grazing species. Grazing species would have evolved a larger mastication surface area and higher-crowned molars in order to grind down the fibrous material in grasses (Fortelius 1985). Mixed-feeder species should occupy an intermediate position between the browser and grazer categories, as their oral morphology should be adapted to both types of vegetation.

2. METHODS

(a) *Definition of variables and data collection*

The variables used in the analyses were selected for their potential functional importance in food selection (incisor breadth, incisor-arcade shape, muzzle width, incisor shape, incisor protrusion), intake rate (incisor breadth) and the processing of food prior to swallowing (occlusal surface, lower permanent molar tooth (M_3) height, M_3 volume, molar-row volume) (Illius & Gordon 1987; Janis 1988; Pérez-Barbería & Gordon 1998*a*,*b*,*c*, 2000). The morphometric traits and the number of species considered (see electronic Appendix A, available on The Royal Society's Web site) were as follows (figure 1): muzzle width (cm, $n = 104$); premolar and molar occlusal surface area (occlusal surface, cm^2, $n = 92$); incisor breadth (cm, $n = 80$; Gordon & Illius 1988); incisor-arcade protrusion (arcade shape, $n = 72$; Illius & Gordon 1987); incisor (I_1/I_3) width ratio (incisor shape, $n = 66$; Janis & Ehrhardt 1988); and incisor protrusion ($n = 25$; Bell 1969).

In the literature there is misinterpretation of incisor protrusion. The original 'index of curvature of the mandibular symphysis' used by Bell (1969) is an indirect measurement of incisor protrusion and correlates negatively with incisor protrusion as measured here. It is useful in museum collections where incisors are usually missing. To avoid further confusion we have used the inverse of this index (figure 1), i.e. the greater the value, the more forward projecting are the incisors.

As indices of hypsodonty we have used three variables from Janis (1988): crown height of M_3 (cm, $n = 113$), volume of M_3 (cm^3, $n = 113$) and the total volume of the post-canine teeth in one half of the lower jaw (molar-row volume, cm^3, $n = 113$)

(details of these measurements can be found in Janis 1988). Specific body masses (kg) were derived for a total of 172 species (Pérez-Barbería & Gordon 1999*a*,*b*), which represents 81% of all living ungulate species (Novak 1991). More details of the museums and institutions which possess the jaws and skulls are given in Pérez-Barbería & Gordon (2000). Feeding styles (browser, mixed feeder, grazer) of individual species were determined following Pérez-Barbería & Gordon (1999*a*).

(b) *Phylogenetic information*

Phylogenetic information for the Ungulata based on a single technique (e.g. molecular or morphological) is not available. Thus, we built a phylogeny using a variety of morphological, palaeontological and molecular sources that provided information for a larger number of ungulate species (see Pérez-Barbería & Gordon 1999*a*,*b*, 2000; Mysterud *et al.* 2001). The unresolved nodes were assumed to be soft polytomies (Purvis & Garland 1993). Since information on branch lengths was not available for all nodes, we used Pagel's (1992) arbitrary method to assign branch lengths (i.e. all internode branch segments of the tree were set to equal one but tips were constrained to be lined up across the top).

(c) *Testing the phylogenetic independence*

There is an ongoing debate regarding whether it is always appropriate to use comparative methods in cross-species analysis to detect adaptive radiations (Abouheif 1999; Harvey & Rambaut 2000). We used the method proposed by Abouheif (1999) to test the assumption of phylogenetic independence before and after applying a comparative method. In this way we tested, first, whether our raw data set needed to be analysed using a comparative approach (i.e. the traits analysed were phylogenetically related), and, second, whether the comparative method used took into account the phylogenetic relatedness efficiently (i.e. after the comparative method was applied, the traits across taxa were not phylogenetically related).

The diagnostic proposed by Abouheif (1999) is based on a measurement of autocorrelation, in the form of a C-statistic, caused by similarity of adjacent phylogenetic observations. This diagnosis cannot be applied to trees that present polytomies (i.e. unresolved nodes, six in our case); therefore, we solved all polytomies using a random-branching criterion. The results presented here were independent of the different branching morphologies generated by the random criterion.

(d) *Independent contrasts*

Independent contrasts for the biological and ecological variables were calculated for the phylogeny described in § 2(b). The oral-morphology traits were $\log_{10}$ transformed, and independent contrasts were then calculated. The three feeding styles considered (browser, mixed feeder and grazer) were transformed into two dummy variables using the mixed-feeder style as the reference category from which independent contrasts were calculated. Independent contrasts assume a Brownian-motion model of character evolution (Felsenstein 1985). The validity of the branch lengths estimated using Pagel's arbitrary method (Pagel 1992) was checked using the Pearson product–moment correlation (not through the origin) between the absolute values of standardized independent contrasts and their standard deviations. The correlations were not significant and, therefore, the branch lengths were appropriate, even under extreme deviations from a Brownian-motion model (Garland *et al.* 1992; Díaz-Uriarte & Garland 1996). The independent contrasts were standardized (by dividing by the square root of the branch lengths) and then used in regression analysis (see § 2(f)). Independent contrasts were carried out with PDAP 5.0 software (Garland *et al.* 1993).

(e) *Plotting independent contrasts*

Recently, Garland & Ives (2000) have developed a methodology that allows independent contrasts to be plotted onto the original space. This method provides a view of independent-contrasts regression lines that is useful for heuristic purposes, although the associated statistics (e.g. intercepts, slopes and standard errors) cannot be used to estimate differences between them (Garland & Ives 2000). We have used this method to plot regression lines for each morphological trait against body mass for each feeding style. For each trait we pruned the populations of browsing, mixed-feeder and grazing species independently, and computed independent contrasts. Finally, we mapped these regression lines back onto the original space using the regression lines predicted by the PDTREE programme (Garland & Ives 2000).

(f) *Statistical analyses*

The use of ratios is not advisable in scaling studies, as their functional significance, when scaled against a covariate, is questionable since the relationship between the components of the ratio and the covariate is masked (LaBarbera 1989). However, we have included three ratios (incisor to shape, incisor to protrusion and arcade to shape) in the analysis because they have previously been used as indices of food-selection ability for species displaying different feeding styles (Bell 1969; Boué 1970; Owen-Smith 1982; Illius & Gordon 1987; Gordon & Illius 1988; Janis & Ehrhardt 1988).

In order to determine differences in the oral traits between feeding styles, we carried out two analyses, one on the original data set, which had been $\log_{10}$ transformed controlling only for the effect of body mass (conventional approach), and the other on the set of independent contrasts determined following analyses controlling for body mass and phylogeny (phylogenetic approach).

In the conventional approach we used accumulated regression analysis to test for differences between feeding styles in the slopes and intercepts of the regression lines (oral traits against body mass). In this approach, the y-axis intercept was fitted in the model, rather than forcing the regressions through the origin (see phylogenetic approach, below). Paired comparisons between feeding styles were carried out using least-significant differences at $\alpha = 0.05$ (Genstat 5 Committee 1993). When traits showed heterogeneity of regressions, then differences in intercepts and slopes between feeding styles were calculated by varying the order in which the feeding styles were added to the model.

Regression analysis based on independent contrasts requires the analysis to be fitted through the origin (Garland *et al.* 1992). In the phylogenetic approach we used accumulated regression analysis through the origin to test for differences in slope between the three feeding styles defined by a set of two dummy variables (see § 2(d)). Consequently, only the slopes were fitted in the model 'body mass + body mass × browser + body mass × grazer'. The overall effect of feeding style was calculated from the accumulated analysis of variance table of the regression analysis by pooling the sum of squares of the feeding-style dummy variables. Paired comparisons between feeding styles were carried out by altering the order in which the two feeding-style dummy variables were fitted, and re-running the regression model (Mysterud *et al.* 2001). In order to compare the

Table 1. *Test of the assumption of phylogenetic independence before and after applying independent contrasts to each of the oral-morphology traits across the species studied (for further details see § 2)*

	before independent contrasts		after independent contrasts	
trait	C-statistic	p	C-statistic	p
body mass	0.738	0.006	0.504	0.057
muzzle width	0.986	0.001	0.110	0.352
molar-row volume	0.496	0.001	0.004	0.449
M_3 height	0.449	0.001	−0.061	0.220
M_3 volume	0.494	0.001	−0.018	0.477
incisor breadth	0.416	0.001	0.026	0.375
occlusal surface	0.215	0.023	0.048	0.190
incisor protrusion	0.323	0.033	−0.197	0.297
incisor shape	0.316	0.001	0.069	0.280
arcade shape	0.376	0.001	0.088	0.473

relative magnitudes of each oral trait across feeding styles we used the estimates of slopes from the regression analysis. Feeding-style dummy variables resulting from independent contrasts become a group of continuous variables that indicates the degree of feeding style for each internal node in the tree. Consequently, predictions of slopes for each feeding style depend on the continuous feeding-style dummy variable chosen in the calculation (Mysterud *et al.* 2001). Accordingly, to avoid ambiguity in the estimates of the slopes, we predicted slopes for dummy variables equal to 1. These slopes cannot be used in a graphic representation of the regression lines (Garland & Ives 2000) but are valid for making relative comparisons between regression lines. Analysis of differences in body mass between feeding styles was carried out using the same regression approach but fitting dummy variables to the model 'browser + grazer'. Statistical analyses were performed using the statistical software package Genstat 5 for Windows release 4.1 (Genstat 5 Committee 1993).

(g) *The effect of sample size*

It is difficult to evaluate the phylogenetic effect across traits because the number of species used in the analysis varies between traits (see § 2(a)). One of the main purposes of this study was to investigate whether body mass has a bigger effect than oral morphology on the characterization of feeding styles. Consequently, we analysed how the variation in the number of species available affected the statistical significance of differences in body mass between feeding styles, since body mass is variable in most species. From the original body-mass data set and using random permutations with replacement, we created sub-populations of between ten and 46 species within a feeding style and then ran regression analysis for each of these sub-populations to detect any differences between feeding styles.

3. RESULTS

(a) *Testing the assumption of phylogenetic independence*

All the traits analysed showed significant phylogenetic correlation between species (table 1). However, all significant correlations disappeared after applying independent contrasts (table 1), which indicates that independent contrasts removed the phylogenetic relatedness efficiently.

(b) *Conventional approach*

All traits, except M_3 volume and arcade shape, exhibited homogeneity of the regression equations ($p \geqslant 0.063$; table 2). Species with different feeding styles differed in body mass ($p < 0.001$), grazers being larger than mixed feeders, which were larger than browsers (table 2).

Grazers had broader muzzles and incisor breadths, more-protruded incisors and greater M_3 height than both mixed feeders and browsers. Browsers and grazers had a wider I_1 in relation to I_3 (incisor shape) than mixed feeders ($p \leqslant 0.05$), but browsers and grazers did not differ from each other in this trait ($p > 0.05$). Consistently, mixed feeders had a larger molar-row volume, greater M_3 height and broader incisors than did browsers (figure 2*a*).

Paired comparisons of regression lines of M_3 volume against body mass between feeding styles indicated that the y-axis intercept of mixed feeders was lower than that of browsers and grazers ($p < 0.001$ in both cases). On the other hand, the slope of M_3 volume was greater in mixed feeders than in browsers ($F_{1,107} = 9.58$, $p = 0.003$). Arcade shape differed in relation to body mass between feeding styles. Grazers had a greater intercept than mixed feeders ($F_{1,66} = 5.09$, $p = 0.027$) and browsers ($F_{1,66} = 6.65$, $p = 0.012$), but the slope of grazers was shallower than those of mixed feeders and browsers ($p \leqslant 0.007$ in both cases; figure 2*a*).

(c) *Phylogenetic approach*

When phylogeny was taken into account, the only traits that differed between feeding styles were body mass, molar-row volume and M_3 height (table 3). Browsers were smaller than grazers and mixed feeders ($p < 0.05$); grazers and mixed feeders did not differ significantly from each other ($p > 0.05$).

Browsers had smaller molar-row volume than grazers and mixed feeders, whilst grazers and mixed feeders did not differ in this trait. Browsers had smaller M_3 heights than grazers, but did not differ from mixed feeders, and mixed feeders did not differ from grazers (table 3 and figure 2*b*).

(d) *The effect of sample size*

The significance of the differences in body mass between feeding styles was not due to a larger sample size for this variable compared with the sample sizes of the other morphological traits. When varying the number of species (between 10 and 46) included in the analysis to detect differences in body mass between feeding styles, only 1 out of the 37 sub-populations produced a non-significant result.

4. DISCUSSION

(a) *Data and analysis*

The results demonstrated that comparative methods need to be applied to analyse this data set and also that the comparative method used was effective in accounting for the effect of phylogeny. This challenges the results of previous studies that did not take phylogeny into account (Bell 1969; Gordon & Illius 1988; Janis & Ehrhardt 1988).

Table 2. *Differences between feeding styles (fs) in body mass (bm) (analysis of variance) and oral-morphology traits (analysis of covariance) in ungulates*

(Abbreviations: s.e.d., standard error of differences; l.s.d., least-significant differences between means ($\alpha = 0.05$); SS, sum of squares; MS, mean square. Paired comparisons between feeding styles based on l.s.d.; b, browser; m, mixed feeder; g, grazer. See § 2(a) for definitions of traits. No s.e.d., l.s.d. or paired comparisons are shown when heterogeneity of the regression lines was detected (M_3 volume, arcade shape) or when there were no significant differences between feeding styles (occlusal surface).)

change	d.f.	SS	MS	*F*	*p*	mean	s.e.d.	l.s.d.	paired comparisons
body mass									
fs	2	12.173	6.087	16.65	< 0.001	2.265	0.12	0.237	g > m > b
residual	169	61.763	0.366			1.85			
total	171	73.936				1.507			
muzzle width									
bm	1	5.827	5.827	715.08	< 0.001	0.573	0.019	0.037	g > m, g > b, m = b
fs	2	0.100	0.050	6.12	0.003	0.516			
bm × fs	2	0.002	0.001	0.15	0.864	0.484			
residual	98	0.799	0.008						
total	103	6.728	0.065						
molar-row volume									
bm	1	47.091	47.091	1192.6	< 0.001	1.278	0.042	0.083	g = m, g > b, m > b
fs	2	0.587	0.294	7.43	< 0.001	1.204			
bm × fs	2	0.224	0.112	2.84	0.063	1.080			
residual	107	4.225	0.039						
total	112	52.127	0.465						
M_3 height									
bm	1	5.319	5.319	257.9	< 0.001	0.563	0.03	0.059	g > m > b
fs	2	1.532	0.766	37.14	< 0.001	0.438			
bm × fs	2	0.101	0.050	2.45	0.091	0.242			
residual	107	2.207	0.021						
total	112	9.159	0.082						
M_3 volume									
bm	1	44.079	44.079	895.82	< 0.001	0.824	—	—	—
fs	2	0.993	0.497	10.09	< 0.001	0.785			
bm × fs	2	0.475	0.238	4.83	0.01	0.592			
residual	107	5.265	0.049						
total	112	50.812	0.454						
incisor breadth									
bm	1	4.889	4.889	1217.9	< 0.001	0.569	0.015	0.03	g > m > b
fs	2	0.096	0.048	11.98	< 0.001	0.518			
bm × fs	2	0.008	0.004	1.05	0.355	0.454			
residual	74	0.297	0.004						
total	79	5.290	0.067						
occlusal surface									
bm	1	10.183	10.183	1376.6	< 0.001	0.738	—	—	g = m = b
fs	2	0.024	0.012	1.6	0.208	0.769			
bm × fs	2	0.005	0.002	0.33	0.718	0.788			
residual	86	0.636	0.007						
total	91	10.848	0.119						
incisor protrusion									
bm	1	0.042	0.042	4.07	0.058	0.241	0.027	0.057	g > m, g > b, m = b
fs	2	0.164	0.082	7.99	0.003	0.078			
bm × fs	2	0.001	0.000	0.03	0.971	0.040			
residual	19	0.195	0.010						
total	24	0.402	0.017						
incisor shape									
bm	1	0.687	0.687	16.37	< 0.001	0.399	0.045	0.09	g > m, g = b, m < b
fs	2	0.334	0.167	3.98	0.024	0.297			
bm × fs	2	0.179	0.090	2.14	0.127	0.458			
residual	60	2.517	0.042						
total	65	3.718	0.057						
arcade shape									
bm	1	0.004	0.004	2.29	0.135	0.150	—	—	—
fs	2	0.013	0.006	3.59	0.033	0.180			
bm × fs	2	0.029	0.015	8.42	< 0.001	0.191			
residual	66	0.115	0.002						
total	71	0.162	0.002						

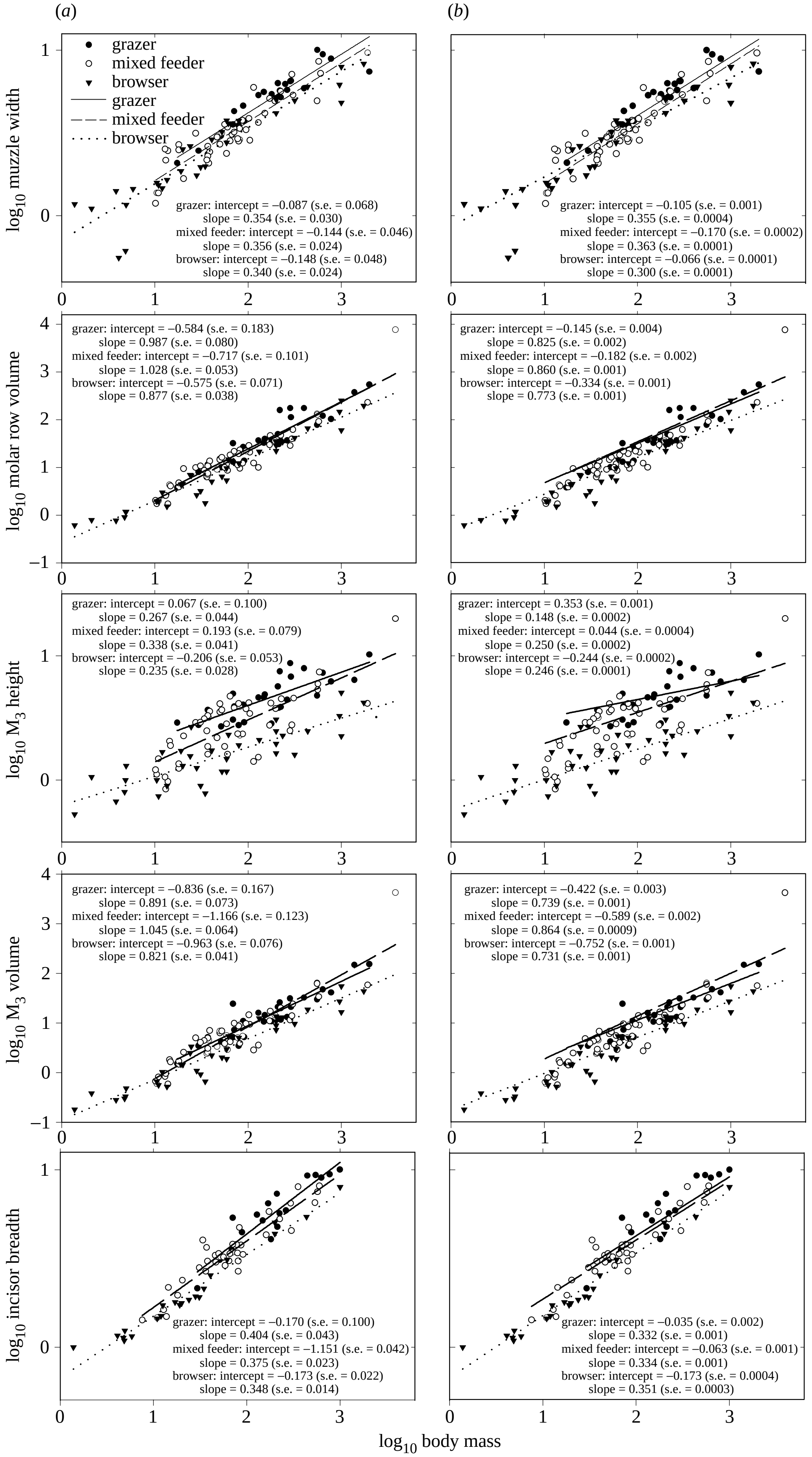
(a)
(b)
grazer
mixed feeder
browser
grazer
mixed feeder
browser
log10 muzzle width
grazer: intercept = –0.087 (s.e. = 0.068)
slope = 0.354 (s.e. = 0.030)
mixed feeder: intercept = –0.144 (s.e. = 0.046)
slope = 0.356 (s.e. = 0.024)
browser: intercept = –0.148 (s.e. = 0.048)
slope = 0.340 (s.e. = 0.024)
grazer: intercept = –0.105 (s.e. = 0.001)
slope = 0.355 (s.e. = 0.0004)
mixed feeder: intercept = –0.170 (s.e. = 0.0002)
slope = 0.363 (s.e. = 0.0001)
browser: intercept = –0.066 (s.e. = 0.0001)
slope = 0.300 (s.e. = 0.0001)
log10 molar row volume
grazer: intercept = –0.584 (s.e. = 0.183)
slope = 0.987 (s.e. = 0.080)
mixed feeder: intercept = –0.717 (s.e. = 0.101)
slope = 1.028 (s.e. = 0.053)
browser: intercept = –0.575 (s.e. = 0.071)
slope = 0.877 (s.e. = 0.038)
grazer: intercept = –0.145 (s.e. = 0.004)
slope = 0.825 (s.e. = 0.002)
mixed feeder: intercept = –0.182 (s.e. = 0.002)
slope = 0.860 (s.e. = 0.001)
browser: intercept = –0.334 (s.e. = 0.001)
slope = 0.773 (s.e. = 0.001)
log10 M3 height
grazer: intercept = 0.067 (s.e. = 0.100)
slope = 0.267 (s.e. = 0.044)
mixed feeder: intercept = 0.193 (s.e. = 0.079)
slope = 0.338 (s.e. = 0.041)
browser: intercept = –0.206 (s.e. = 0.053)
slope = 0.235 (s.e. = 0.028)
grazer: intercept = 0.353 (s.e. = 0.001)
slope = 0.148 (s.e. = 0.0002)
mixed feeder: intercept = 0.044 (s.e. = 0.0004)
slope = 0.250 (s.e. = 0.0002)
browser: intercept = –0.244 (s.e. = 0.0002)
slope = 0.246 (s.e. = 0.0001)
log10 M3 volume
grazer: intercept = –0.836 (s.e. = 0.167)
slope = 0.891 (s.e. = 0.073)
mixed feeder: intercept = –1.166 (s.e. = 0.123)
slope = 1.045 (s.e. = 0.064)
browser: intercept = –0.963 (s.e. = 0.076)
slope = 0.821 (s.e. = 0.041)
grazer: intercept = –0.422 (s.e. = 0.003)
slope = 0.739 (s.e. = 0.001)
mixed feeder: intercept = –0.589 (s.e. = 0.002)
slope = 0.864 (s.e. = 0.0009)
browser: intercept = –0.752 (s.e. = 0.001)
slope = 0.731 (s.e. = 0.001)
log10 incisor breadth
grazer: intercept = –0.170 (s.e. = 0.100)
slope = 0.404 (s.e. = 0.043)
mixed feeder: intercept = –1.151 (s.e. = 0.042)
slope = 0.375 (s.e. = 0.023)
browser: intercept = –0.173 (s.e. = 0.022)
slope = 0.348 (s.e. = 0.014)
grazer: intercept = –0.035 (s.e. = 0.002)
slope = 0.332 (s.e. = 0.001)
mixed feeder: intercept = –0.063 (s.e. = 0.001)
slope = 0.334 (s.e. = 0.001)
browser: intercept = –0.173 (s.e. = 0.0004)
slope = 0.351 (s.e. = 0.0003)
log10 body mass
0
1
2
3
4
–1

Figure 2. (*Cont.*)

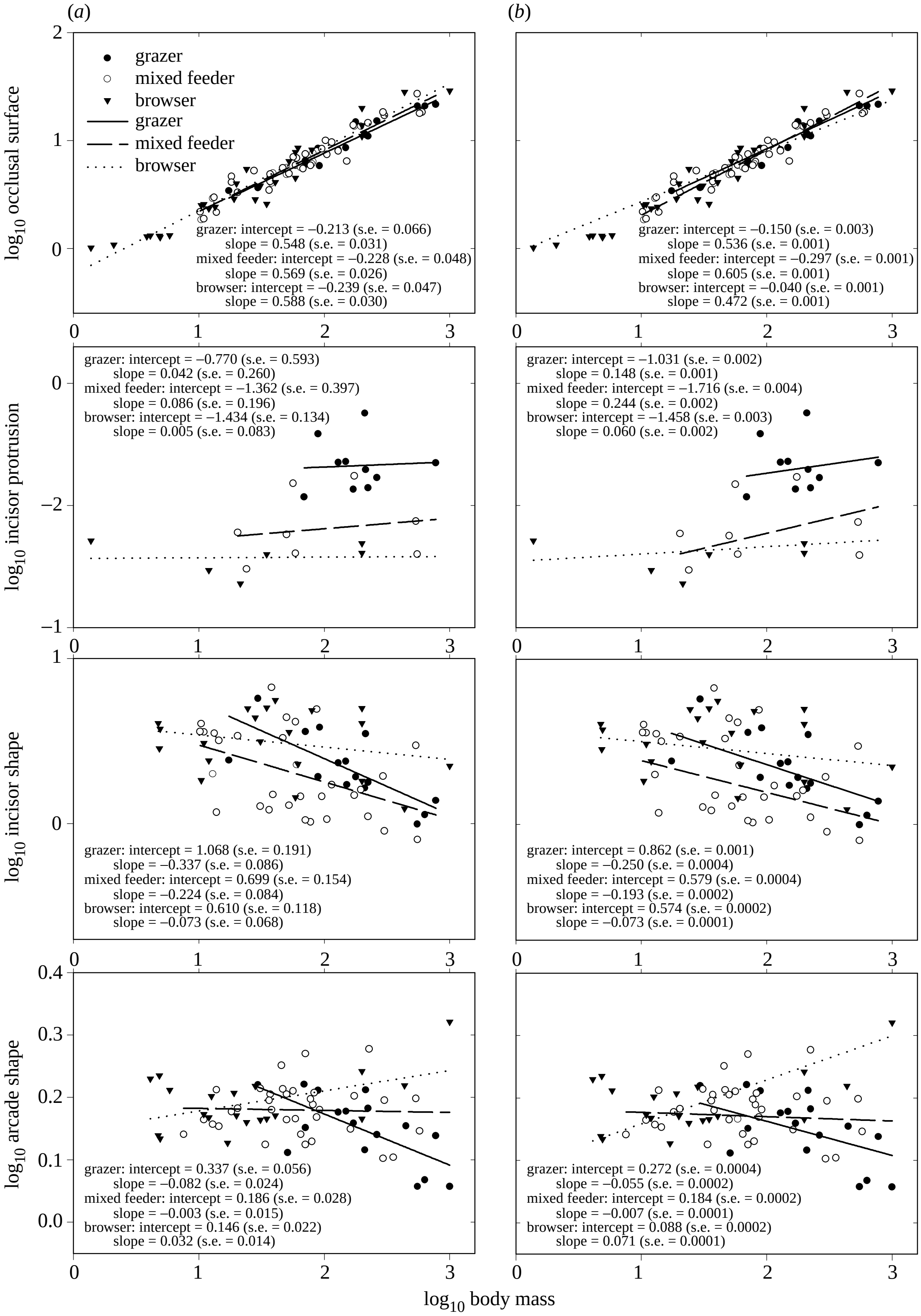

Figure 2. (Opposite and above.) Body mass ($\log_{10}$ transformed) plotted against nine traits of the oral morphology of ungulate species that differ in body size: (*a*) conventional approach; (*b*) phylogenetic approach. Independent contrasts plot back onto the original space. See § 2 for further details and definitions of the oral traits.

Table 3. *Differences between feeding styles in body mass and some traits of oral morphology in ungulates when both phylogeny and body mass are taken into account*

(Covariate–body mass: effect of body mass. Feeding style: differences between feeding styles (pooled). See § 2(a) for definitions of traits.)

	covariate–body mass			feeding style			
	F	d.f.	*p*	*F*	d.f.	*p*	paired comparisons
body mass	—	—	—	7.23	2,169	0.001	g = m, m > b, g > b
muzzle width	373.28	1,100	< 0.001	2.15	2,100	0.122	—
molar-row volume	447.55	1,109	< 0.001	4.00	2,109	0.021	g = m, m > b, g > b
M_3 height	62.8	1,109	< 0.001	4.52	2,109	0.013	g = m, m = b, g > b
M_3 volume	324.35	1,109	< 0.001	2.41	2,109	0.095	—
incisor breadth	326.66	1,76	< 0.001	0.13	2,76	0.883	—
occlusal surface	477.0	1,88	< 0.001	0.88	2,88	0.418	—
incisor protrusion	4.83	1,21	0.039	1.06	2,21	0.364	—
incisor shape	16.92	1,62	0.001	0.37	2,62	0.700	—
arcade shape	0.91	1,68	0.344	0.62	2,68	0.544	—

Prior to discussing the results, it is prudent to discuss the quality of the data set and the possible loss of power of our analysis at each step. The first two considerations are the sources of error implicit in the traits and the criterion of assigning each species to a feeding style. These two issues have frequently been overlooked in previous studies that analysed morpho-physiological differences between feeding styles in the Ungulata. The most striking source of error is that the estimate of body mass and the measurements of the oral-morphology traits studied do not come from the same specimens (see § 2(a)). The body-mass variability between different populations of the same species can be of the same order of magnitude as, or higher than, the variation between species (Silva & Downing 1995). Since it was not possible to identify the specific population source of all specimens in which the morphological traits were measured, as many animals as possible from different populations were included in our body-mass data file in order to reduce the variability due to randomness in sampling.

Given the high variability in dietary composition, assigning species to the three feeding styles is difficult and in many cases may result in oversimplification. For example, the eland (*Tragelaphus oryx*) has been shown, in some studies, to be a browsing species, with 77% of its diet composed of 'browse' (Van Zyl 1965), whereas in other studies (Nge'the & Box 1976) less than 30% of its diet has been reported to be 'browse'. However, this source of error is not inherent only in our study, it affects any study that involves similar feeding-style categorization.

Care has to be taken when comparing the results obtained across the traits studied, because the sample size and the species included in the analyses vary between traits. However, the results presented here allow us to challenge previous analyses reported in the literature because our analyses use mainly the same data sets as previous studies.

(b) *What morphological traits characterize differences in feeding styles?*

After controlling solely for body size there was, in general, good agreement between the results of previous studies (see § 1) and the results presented here. Grazers were dominated by large species with broader muzzles and incisors, their incisors protruded more from the incisor arcade and their molars were bulkier and taller than those of mixed feeders and browsers. However, contrary to our prediction, incisor shape did not differ between browsers and grazers; in fact, mixed feeders had narrower central incisors than did grazers or browsers.

Other phylogenetic analyses that have dealt with differences between feeding styles in ungulates (Pérez-Barbería & Gordon 1999*a*,*b*; Mysterud *et al.* 2001) have also concluded that body mass is far more important in explaining the differences between feeding styles than many morphological and behavioural traits. Despite the wide overlap in the body-mass range between feeding styles, body mass is associated with different dietary habits. Additional evidence further supports the importance of body mass in food-selection ability. For example, Nge'the & Box (1976) found that goats (46 kg) were more skilled at selecting *Acacia tortilis* leaves and avoiding the spines of this species than were eland (532 kg); both species are included in the mixed-feeder category. Likewise, Cooper & Owen-Smith (1986) found that plant spinescence had much less effect on the intake of plant material by small herbivore species, such as goats (35 kg) and impala (*Aepyceros melampus*, 50 kg), than by larger species, such as the kudu (*Tragelaphus strepsiceros*, 180 kg). In both studies obvious differences in body mass lead to absolute differences in muzzle size, which can explain the interspecific differences in food-selection ability.

Although much attention has been paid to how oral morphology is related to intake rate and food selection (i.e. muzzle width, incisor breadth, arcade shape, incisor shape: Boué 1970; Jarman 1974; Cutton-Brock & Harvey 1983; Gordon & Illius 1988; Janis & Ehrhardt 1988; Illius & Gordon 1990; Weckerly & Nelson 1990), none of the traits examined showed significant differences between feeding styles after controlling for phylogeny. However, body mass and two traits related to hypsodonty (molar-row volume and M_3 height) retained significant differences between feeding styles after taking phylogeny into account. Browsers were still significantly smaller than grazers and mixed feeders; grazers and mixed feeders did not differ in body mass. Molar-row volume and M_3

height were smaller in browsers than in grazers and mixed feeders; there was no significant difference in these traits between grazers and mixed feeders. The adaptive relationship between hypsodonty and grazing (grazing species have to grind coarse vegetation and vegetation contaminated with soil) has been widely accepted in the literature (Fortelius 1985; Janis 1988) and our results support this hypothesis. It seems reasonable on the grounds that dental tissues (enamel, cement and dentine) are homogeneous across ungulates (Fortelius 1985), so adaptation to abrasive diets has to be achieved by increasing tooth growth rate (as happens in the incisors of rodents) or by increasing the volume of the teeth involved in mastication, as our results indicate.

The general thinking about the relationship between incisor-arcade shape and food selection relies on the conceptual model of preferred individual items of food within a matrix of thorns or low-quality food. However, this may not be the general case, browsers can also frequently face situations where items of food are distributed homogeneously or clumped in patches, and in these cases the grazer-type incisor breadth would be more efficient. On the other hand, and as a general rule, browsers face less abrasive diets than grazers, although there are some exceptions, in that some species of browsers feed on fruits and seeds with hard exocarps. This could explain why oral traits related to intake and food selection are less conspicuous than hypsodonty, and suggests that the actual food-selection process is similar for similarly sized species of browsers and grazers, but food processing is different. This emphasizes the importance of the structural properties of food in defining oral morphology.

It has been claimed that the clustering tendency of some categories of discrete variables over the phylogenetic tree causes a loss of statistical power in comparative analyses (i.e. the bigger the clustering pattern among categories, the bigger the required statistical test value has to be in order to detect significant differences between these categories; Vanhooydonck & Van Damme 1999). However, it is argued that species that cluster together will tend to share morphological and behavioural traits simply because they share common ancestors, which is the main rationale of the comparative method (Felsenstein 1985). It is also possible that the divergence in mouth morphology between feeding styles occurred in the late Miocene during the main radiation of ungulates (Janis 1982). Our results demonstrate that only body mass and hypsodonty explain differences between feeding styles once phylogeny has been taken into account. Consequently, it seems clear that body size is the main variable that characterizes differences between species with different dietary habits. Its effect is more important than the feeding style or the variation in mouth morphology associated with the phylogenetic branching pattern, negating, in most cases, the significance of the dietary-adaptation effect claimed in previous studies (Boué 1970; Gordon & Illius 1988; Janis & Ehrhardt 1988; Janis & Constable 1993).

(c) *Why are morpho-physiological differences between feeding styles not extreme among ungulates?*

For medium- and large-sized species, such as the ungulates (ranging from 1.5 kg to more than 1000 kg), plants provide a low-quality food resource. Extreme selection of some highly nutritious parts of the plants or their products (e.g. nectar) cannot be exploited efficiently by species with body masses as high as those of the ungulates. As a rule, most herbivorous species have to ingest a large amount of low-quality vegetable food. Thus, behavioural and morphological adaptations that maximize intake rates seem to be common for most ungulate species, as our results indicate. It should be pointed out that adaptation to food selection could occur in the soft parts of the mouth (i.e. muzzle, lips, tongue) rather than in the bone structures.

Out of the species considered in this study, 49% belonged to the mixed-feeder category while only 21% were grazers and 30% were browsers. This difference is accentuated when feeding styles are analysed by biogeographical regions. In our data set, 68 and 103 species inhabit temperate and tropical regions, respectively. In the temperate region, where seasonal changes in vegetation abundance and quality are large, 79% of the species are mixed feeders, but in the tropical region only 36% fall into this category. Most of the environments occupied by ungulates show a clear seasonal change in the abundance and quality of vegetation (Gwynne & Bell 1968; Bell 1969; Owen-Smith 1982). In such environments it seems reasonable to hypothesize that evolution has not favoured extreme morphological traits specifically adapted to a narrow range of food resources. The lack of feeding-style differences in most of the morphological traits studied is consistent with this hypothesis.

5. CONCLUSIONS

After controlling for phylogeny, browsers, on average, were smaller in body size and exhibited smaller indices of hypsodonty than did grazers and mixed feeders. Evolution seems to have selected for an association between feeding style and body mass as compared with phylogeny. This appears to stem from the fact that variation in body mass provides a more integrated response to multiple functions associated with ungulate feeding than would an adaptation in mouth morphology alone. The fact that feeding styles can be distinguished from each other in their degree of hypsodonty suggests that the food-selection processes are similar for equally sized species of different feeding styles but that food processing is different.

We thank C. M. Janis for the data on muzzle width, occlusal surface and diet and for advice throughout the study, although she does not share our enthusiasm about the method. We also thank T. Garland, N. Owen-Smith, G. R. Iason, J. Byers, S. B. Emerson, J. A. Milne and three anonymous referees for advice and comments on the manuscript. The senior author thanks C. Nores for his support. This paper was supported by funding from Training and Mobility of Researchers of the European Communities and The Scottish Executive Rural Affairs Department.

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