

Differences in body mass and oral morphology between the sexes in the Artiodactyla: Evolutionary relationships with sexual segregation

F. Javier Pérez-Barbería^{1,2} and Iain J. Gordon^{1*}

¹*The Macaulay Land Use Research Institute, Craigiebuckler, Aberdeen AB15 8QH, UK and*

²*Instituto de Recursos Naturales y Ordenación del Territorio, 13 Independencia, Oviedo 33071, Spain*

ABSTRACT

It has been hypothesized that the evolution of sexual dimorphism could lead to sexual dimorphism in trophic structures, mainly the mouthparts, through inter-sexual niche partitioning. This hypothesis is based on the assumption that females select habitats on the basis of their requirements for diets with high nutrient concentrations (due to pregnancy and lactation), whereas males select for habitats with abundant resources (due to their larger body size and higher absolute nutrient requirement). We analysed a data set of the morphological traits of the mouth and teeth, which have been proposed as being functionally related to food selection ability (muzzle width, incisor protrusion), food comminution (molar occlusal surface area) and intake (incisor breadth), in males and females of species from the mammalian order Artiodactyla. Our analyses showed that all of the morphological traits studied covaried isometrically with body mass. The effect of sharing common ancestors did not have a significant effect on oral morphology, which indicates that oral morphology evolved in parallel in both sexes. We detected differences in body mass between the sexes and these differences remained when phylogeny was taken into account. Our results demonstrate that the dimensions of the oral traits result primarily from differences in body mass between the sexes rather than differences in niche adaptation between the sexes. The relationship between sexual dimorphism in body mass and differences in niche partitioning between the sexes in the Artiodactyla is discussed.

Keywords: allometry, body mass, comminution, comparative method, food selection, intake.

INTRODUCTION

It is unclear whether allometric differences in oral morphology are in part responsible for the observed differences in habitat and diet selection between the sexes in ungulates (Pérez-Barbería and Gordon, 1998a). Some studies have indicated that differences in oral morphology between the sexes, after controlling for body mass, are the main cause of resource partition. For example, Shine (1989) reviewed the evidence for inter-sexual niche partitioning resulting in selection for sexual dimorphism in trophic structures, such as the

* Author to whom all correspondence should be addressed. e-mail: i.gordon@mluri.sari.ac.uk
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mouthparts, and found that, in artiodactyls, the mandibles of females were larger than those of males (Goldspink, 1981; Bartosiewicz, 1987). This difference in mandible morphology was thought to result in females having higher forage intake rates than males in relation to their body mass. Similarly, Kay (1978) suggested that female cercopithecids have larger teeth than males in relation to body mass, which would result in higher rates of food comminution (Fortelius, 1985; Shipley *et al.*, 1994; Pérez-Barbería and Gordon, 1998b) and, therefore, nutrient acquisition, since females have higher relative energy requirements than males due to pregnancy and lactation (but see Clutton-Brock, 1991). Other studies found no differences in oral morphology between the sexes, after controlling for body mass, but suggested that, in sexually dimorphic species, differences in body mass could be the source of differences in diet selection between the sexes (Illius and Gordon, 1990; Pérez-Barbería and Gordon, 1998a). For example, in red deer (*Cervus elaphus*), Illius and Gordon (1990) found no differences in incisor breadth between the sexes, after controlling for body mass. Because incisor breadth scales isometrically with body mass ($M^{0.33}$, $M^{0.40}$ for 26 and 89 species of ruminants, respectively; Clutton-Brock and Harvey, 1983; Gordon and Illius, 1988), it has been suggested that differences in food selection between the sexes, in species that display sexual dimorphism in body mass, may be due to the body size effect. However, these studies did not consider how the effect of sharing common ancestors or the actual adaptation process explain the variation in oral morphology and body mass between the sexes. This is of paramount importance if we wish to determine how the differences in the trait evolved between the sexes (Felsenstein, 1985; Harvey and Pagel, 1991; Garland *et al.*, 1993).

We use concepts from feeding strategy theory derived from inter-specific studies of ungulates and apply these to differences in oral morphology between the sexes. This theory suggests that wider mouths favour increased intake rates, whereas narrower muzzles and more protrusive incisors facilitate the grasping of small items of high-quality food from an intimate mixture of vegetation (Bell, 1969; Gordon and Illius, 1988; Janis and Ehrhardt, 1988). Intake rate can also be increased by a larger molar surface, which facilitates food comminution (Pérez-Barbería and Gordon, 1998b).

The aim of this study was to establish whether the sexes differ in oral morphology, after body mass and phylogeny have been taken into account. We hypothesized that one of the following assumptions should be corroborated:

1. In contrast to previous hypotheses, females should have an oral morphology that enables them to feed selectively, grasping small, high-quality food items (i.e. females have a narrower incisor breadth and muzzle, and a more protrusive incisor arcade, relative to body mass than males). On the other hand, males should have a wider mouth and larger post-canine mastication surface that enables them to process larger quantities of coarse diets.
2. Female and male oral morphology scales isometrically with body mass, but body mass differs across the sexes when phylogeny is taken into account.

METHODS

Definitions of variables and data collection

The variables used in our analyses were selected for their potential functional significance in food selection (incisor breadth, incisor protrusion, muzzle width), intake (incisor breadth)

and the ability to grind food prior to swallowing (occlusal surface area) (Illius and Gordon, 1987; Pérez-Barbería and Gordon, 1998a,b,c). We took measurements of four morphometric traits of the mouth (see below) of species of artiodactyl from the mandibles and skulls of at least three individuals of each sex. The number of species available in the data set varied across the different traits, as it was not possible to achieve a complete data set of all traits for all species studied. Thus, to include the greatest number of species, we decided to use the full available data set for each trait. The morphometric traits and the number of species included (see the Appendix) in the data set were as follows: muzzle width (cm, $n = 92$), measured at the junction between the maxillary and premaxillary bones; premolar and molar occlusal surface area (cm², $n = 92$), obtained by multiplying the length (mesio-distal diameter) by the width (buccolingual diameter) of each post-canine tooth of one ramus of the mandible and then summing the values; incisor breadth (cm, $n = 47$), measured as the distance between the outermost points of the incisiform canines C_1 of each ramus (Illius and Gordon, 1987); incisor protrusion (cm, $n = 38$), measured as the perpendicular distance to the front of the incisor arcade from a line between both canines. Incisor protrusion was not measured directly, but was estimated using incisor breadth and the distance around the incisor arcade from the canines on each side, and assuming a parabola for the shape of the incisor arcade (A.W. Illius, personal communication). Only individuals that had a full set of permanent teeth, but which did not show excessive dental wear (i.e. no more than 30% of the occlusal surface of the second molars worn to reveal the dentine), were included in the analysis. All specimens were originally collected in the wild and came from the following institutions: British Museum (Natural History), London, UK; Museum of Comparative Zoology, Harvard University, Cambridge, MA, USA; Museum of Comparative Zoology, Cambridge University, Cambridge, UK; National Museum of Kenya, Nairobi, Kenya; Museum of Cape Town University, Cape Town, South Africa; and Transvaal Museum, Pretoria, South Africa.

We carried out an extensive bibliographic search to derive a data set of body mass (kg) that comprised as much information as possible about population and subspecies variability for the species of artiodactyl used in the analyses. Information for different populations or subspecies was pooled and the weighted average calculated for each species. When the literature did not provide the sample size of specimens weighed, we assumed a conservative value of $n = 1$, and when the literature only gave a body mass range, we assumed a sample size of $n = 2$. Body masses were derived for a total of 144 species (see the Appendix), which comprise 68% of total extant artiodactyl species (Novak, 1991).

Phylogenetic information

Unfortunately, no complete phylogeny for the extant Ungulata existed that was based on one only method of derivation (e.g. morphology or molecular techniques); therefore, phylogenies for studies that comprise a large number of species had to be constructed using a number of different phylogenetic studies (e.g. ungulates: Pérez-Barbería and Gordon, 1999a; lizards: Wiens, 1999). Our phylogeny is based mainly on Pérez-Barbería and Gordon (1999a), who compiled information from a variety of sources (Kingdon, 1982; Corbet and Hill, 1986; Janis and Scott, 1987, 1988; Gentry and Hooker, 1988; Novak, 1991; Gentry, 1992; Garland and Janis, 1993; Essop *et al.*, 1997). Information on branch lengths was not available for all nodes and, in a number of cases, significant discrepancies occurred between divergence times estimated by the palaeontological and molecular techniques. Therefore, we

used Grafen's (1989) arbitrary method to assign branch lengths. Adequate standardization of the contrasts was checked as described below. The method assumes that the expected variance of change along a branch is proportional to its length (i.e. Brownian motion model), and confers to each branch node a height equal to the number of species at or below the node minus one. The final arbitrary branch length is estimated as the difference in height between the top and the bottom of the node.

The comparative method and statistical analysis

The hierarchical structure of the phylogeny results in a set of species that cannot be considered to be statistically independent (Felsenstein, 1985; Harvey and Pagel, 1991). To compare the amount of variation accounted for by sex from the raw data set (i.e. phylogeny plus adaptation) and from the purely adaptational effect (i.e. when the effect of sharing common ancestors is removed, see below), we proceeded as follows. First, the residuals from regressing each trait against body mass for each sex were estimated using least squares regression; then, the residuals of females were regressed against the residuals of males for each trait using Model II regression (see below) and the deviation of slope = 1.0 was tested ($\alpha = 0.05$). Second, independent contrasts (Felsenstein, 1985) were used to assess sexual dimorphism in the oral traits and body mass, as described in Garland *et al.* (1992) and Abouheif and Fairbairn (1997), for the adaptational effect.

Before carrying out the analyses, all traits were $\log_{10}$ -transformed to produce linear relationships between the traits and the covariate. The unresolved nodes were assumed to be soft polytomies, using $n - 1$ contrasts and $c - 1$ degrees of freedom throughout the analyses (Purvis and Garland, 1993), where n is the number of species and c is the number of nodes. Independent contrasts assume a Brownian motion model of character evolution (Felsenstein, 1985), and violation of this assumption may result in inflated type I error rates. However, Díaz-Uriarte and Garland (1996) demonstrated that, even under extreme deviations from a Brownian motion model, if branch lengths are properly transformed, the maximum observed type I error never exceeds 0.1 for a nominal significance level of 0.05 (but see Harvey and Rambaut, in press). We checked the validity of the branch lengths estimated using Grafen's (1989) arbitrary method, by plotting the absolute value of each standardized contrast against its standard deviation (i.e. the square root of the sum of its branch lengths; Garland *et al.*, 1992). Significant Pearson product-moment correlations were found for all variables ($P < 0.05$), indicating that the standardization process was not appropriate. Appropriate standardization was achieved by transforming the branch lengths using the power $\rho = 0.5$ (Grafen, 1989). This value was chosen by checking ρ between 0 and 1 in increments of 0.1 and using the value that gave the lowest non-significant Pearson correlation coefficient ($P > 0.135$ for all cases) in the diagnostic of Garland *et al.* (1992). We controlled for the effect of body mass by using the residuals of the Model I regression (least squares) through the origin of the positivized contrasts of the trait against the contrasts of body mass [i.e. changing the sign of the negative contrasts found in the x -variable (body mass) and simultaneously switching the sign of those y -variable contrasts whose x -variable was initially negative (Garland *et al.*, 1992)]. Model I regression was used instead of Model II regression, since only the former offers residuals free of the effect of the y -variable (Sokal and Rohlf, 1995). Residuals were inspected for outliers and, after their removal, the regression line interception at the origin was verified with the rest of the contrasts ($P \geq 0.319$ in all cases). The final number of species used in the

analyses was as follows: 88, 89, 45, 34 and 143 for muzzle width, occlusal surface area, incisor breadth, incisor protrusion and body mass, respectively.

Sexual dimorphism in the traits studied was assessed using Model II regression (Rayner, 1985; McArdle, 1988; LaBarbera, 1989) of the female residuals for a trait (y-axis) against the male residuals for that trait (x-axis), following the axes allocation convention of Abouheif and Fairbairn (1997). We chose Reduced Major Axis (RMA) Model II regression because similar rates of error are conferred to dependent and independent variables, and in our data set the error rates for both variables were unknown and the two variables to be regressed differed in size (Sokal and Rohlf, 1995). When the slope of the regression is significantly greater than 1.0, the female trait is allometrically greater than that of the male; when the slope is less than 1.0, the male trait is allometrically greater than that of the female, and both sexes are isometric for the trait when the slope does not differ from 1.0. Sexual dimorphism in body mass was assessed by inspection of the RMA slope of the independent contrasts of the body mass of males against the independent contrasts of the body mass of females, as indicated above.

We also tested for sexual dimorphism in body mass and traits using *t*-tests for paired comparisons between the sexes. In the case of sexual dimorphism in body mass, the independent contrasts of male versus female body mass were used. In the case of sexual dimorphism in the oral morphology traits, we used the residuals for each sex of the independent contrasts of body mass against morphological traits. This method tests whether the mean of the differences between the sexes differs from zero, where zero means isomorphism (Sokal and Rohlf, 1995).

Independent contrasts were carried out with PDAP software (Garland *et al.*, 1993). Statistical analyses were performed using the SPSS for Windows release 5.0.1 statistical software package (Norušis, 1990).

RESULTS

The combined effect of phylogeny and adaptation

When body mass was not taken into account, all of the oral traits studied had a slope of the relationship between the male trait and the female trait of significantly less than 1.0 (slopes between 0.598 and 0.978, $P < 0.05$; Table 1), and because the regression was forced throughout the origin, this indicates that, across species, all traits studied were larger in males than in females. However, when body mass was taken into account, males and females did not differ in the size of any trait of oral morphology (slopes between 0.996 and 1.006; Table 1).

Sexual dimorphism in morphological oral traits and body mass: The effect of adaptation

After controlling for phylogeny and body mass, incisor protrusion was the only parameter for which there was no significant correlation between males and females ($r = 0.297$, $F_{1,32} = 3.09$, $P = 0.089$). The other three traits – muzzle width, occlusal surface area and incisor breadth – showed significant correlations between the sexes (Table 2). Moreover, the slopes obtained were not significantly different from 1.0 (Table 2). This indicates that all morphological traits studied scaled isometrically between the sexes. The regression line obtained between male and female body mass resulted in a highly significant regression

Table 1. Sexual dimorphism in muzzle width (MZW), occlusal surface area (OSA), incisor breadth (IB) and incisor protrusion (IP) $\log_{10}$ -transformed across artiodactyl species

		Not controlling for body mass					Controlling for body mass				
	<i>n</i>	r^2	p_r	Slope	95% confidence limits (slope)	Sexual dimorphism ^a	r^2	p_r	Slope	95% confidence limits (slope)	Sexual dimorphism ^a
MZW	92	0.978	<0.001	0.925	0.912–0.938	male > female	0.797	<0.001	1.000	0.907–1.094	no
OSA	92	0.990	<0.001	0.978	0.970–0.987	male > female	0.606	<0.001	1.006	0.734–1.277	no
IB	38	0.947	<0.001	0.910	0.876–0.944	male > female	0.523	<0.001	1.001	0.794–1.209	no
IP	47	0.832	<0.001	0.598	0.467–0.730	male > female	0.166	0.012	0.996	0.683–1.308	no

Note: The hypothesis tested was that the slope through the origin of the male trait (x-axis) against female trait (y-axis) differs from 1.0. Model II (Reduced Major Axis) regression was used. *n* = number of species, p_r = significance of the variance accounted for, r^2 .

^a Sexual dimorphism: slope significantly less than 1.0 = male trait larger than that of female; slope significantly greater than 1.0 = male trait less than that of female. No sexual dimorphism: slope does not differ from 1.0 ($\alpha = 0.05$).

Table 2. Sexual dimorphism in muzzle width (MZW), occlusal surface area (OSA), incisor breadth (IB), incisor protrusion (IP) and body mass (M) across artiodactyl species (after accounting for phylogeny, using independent contrasts; see Methods for details)

Reduced Major Axis regression					<i>t</i> -test	
n_c	r	p_r	Slope	95% confidence limits (slope)	t_{n_c-1}	Sexual dimorphism
MZW	0.779	<0.001	1.066	0.926–1.207	0.67	no
OSA	0.698	<0.001	0.954	0.806–1.103	0.52	no
IB	0.709	<0.001	0.884	0.657–1.112	–1.59	no
IP	0.297	0.089	0.561	^a	0.08	no
M	0.979	<0.001	0.906	0.875–0.937	3.77	male > female

Note: Sexual dimorphism was also tested using *t*-tests for paired comparisons. This analysis tests whether the mean of the differences of the independent contrasts of both sexes differs from zero. A mean of zero indicates isomorphism. n_c = number of independent contrasts; p = significance value associated with *t*-test; p_r = significance of the variance accounted for, r^2 .

^a Confidence limits for the slope were not estimated because the regression was not significant.

($r = 0.979$, $F_{1,141} = 3303.8$, $P < 0.00005$) and sexual dimorphism in body mass was detected (Table 2), with males being larger than females. These results were consistent with the t -tests for paired comparisons for all oral morphology traits ($P \geq 0.119$) and body mass ($P < 0.0005$; Table 2).

DISCUSSION

Differences in body mass between the sexes versus isometry in oral morphology

Our cross-species analysis clearly refutes previous evidence of differences in oral morphology between the sexes. Our results indicate that variation in the size of the oral morphology between the sexes can be attributed exclusively to differences in body mass between the sexes, because the differences in oral morphology disappeared when body mass was taken into account. Similar results were obtained when phylogeny was taken into account – that is, the size of all traits varied isometrically with body mass. However, differences in body mass between the sexes remained significant after removing the effect of sharing common ancestors. This indicates that oral morphology has evolved in parallel in males and females, but body mass has diverged, favouring an increase in size in males. Other studies using the comparative method have found consistently that a significant amount of the variation in the traits studied is due to the effect of sharing common ancestors – for example, mandible bone morphology and activity time related to feeding strategies in ungulates (Pérez-Barbería and Gordon, 1999a,b), maximal running speed in cursorial mammals (Garland and Janis, 1993), and cost of reproduction in canids (Geffen *et al.*, 1996). However, in the present study, the variation in oral morphology accounted for by phylogeny was clearly overridden by the effect of body mass, which was able to explain all differences in oral morphology between the sexes.

Evolution seems to have operated on body mass variation to a greater extent than other morphological traits of ungulates. It appears this is because body mass covaries with most of the biological and ecological functions of animal life (see Peters, 1983). Thus any modification to body mass through natural selection presents more of an opportunity for multi-functional adaptation than alteration of a particular trait, although exceptions are seen in the development of sexual secondary characters, such as horns or antlers (Geist and Bayer, 1988).

Sexual dimorphism in body mass and inter-sexual niche partitioning

Differences in habitat use between the sexes have been observed in many species of ungulates (Novak, 1991); several hypotheses have been proposed to account for this (Bon and Campan, 1996; Main *et al.*, 1996). One of these, the sexual dimorphism–body size hypothesis (for reviews, see Miquelle *et al.*, 1992; Bon and Campan, 1996; Main *et al.*, 1996; Gross, 1998; Main, 1998), is based on three sub-hypotheses (Pérez-Barbería and Gordon, 1999c): '(i) that in dimorphic species males, the larger sex, have relatively smaller bite sizes on short swards and they are less selective feeders because of their greater daily requirements for food, (ii) they (*males*) move off to feed on taller swards, which provide sufficient volume/bulk of food but are of poorer quality, and (iii) they (*males*) can subsist better on poorer quality swards since they are more efficient digestors of fibre'. However, the assumption of sexual dimorphism in body size, free of the effect of phylogeny, has not

previously been demonstrated in artiodactyls (Weckerly, 1998). Using a similar comparative method to that used in the present study, Abouheif and Fairbairn (1997) found weak but statistically non-significant sexual dimorphism in body mass (female < male) across 27 species of perissodactyls and artiodactyls. Using nested analysis of variance on five levels of ungulate taxonomy, Loison *et al.* (1999) detected sexual dimorphism in body mass in ungulates. However, they did not control satisfactorily for the effect of phylogeny, because the taxonomy did not describe the phylogenetic relationships between species (Harvey and Pagel, 1991). Our results support the sexual dimorphism–body size hypothesis as a general rule to explain sexual segregation in artiodactyls. We have shown that no allometric differences in oral morphology exist between the sexes, suggesting that sub-hypothesis (i) above is merely a consequence of differences in body size between the sexes. Sub-hypotheses (ii) and (iii) also require that males are larger than females, which we have demonstrated.

Avoidance or relaxation of competition for food between the sexes has been suggested to be an advantage of sexual segregation within species (Main *et al.*, 1996). Sexual divergence in oral morphology would be a useful mechanism for promoting differences in niche occupation between the sexes in artiodactyls (Shine, 1989); however, evolution has favoured dimorphism in body size rather than dimorphism in oral morphology. The absolute difference in size of oral morphology between the sexes, resulting from differences in body size, provides the mechanism to allow the use of different food resources and, therefore, favours differences in habitat partitioning between the sexes. However, there is evidence that avoidance of competition between the sexes has not been the main selection force for the evolution of sexual dimorphism. It has been demonstrated that sexual dimorphism evolved in response to polygyny, and that polygyny was triggered by occupancy of open habitats (F.J. Pérez-Barbería, I.J. Gordon and M. Pagel, unpublished results). From this, a counterintuitive effect appears to exist; that is, occupancy of open habitats increases the aggregation of individuals and favours polygyny, and sexual dimorphism evolves because a larger body size confers advantages during fights between males for breeding access to females in polygynous mating systems. Subsequently, sexual dimorphism favours sexual segregation because of the differences between the sexes in the efficiency of selecting and digesting food. However, sexual segregation could also favour increased levels of polygyny, because it focuses competition between males for access to females only during the short mating season, which is energetically affordable, rather than over prolonged periods, which occurs in mating systems such as resource or harem defence polygyny.

Whatever the cause of habitat partitioning, dimorphism in body mass by itself could favour the use of different food resources without any other foraging specialization having to be invoked.

ACKNOWLEDGEMENTS

We thank C.M. Janis for providing advice throughout the study; P. Harvey, G.R. Iason, J. Byers, S.B. Emerson and J.A. Milne for advice and comments on the manuscript; and T. Garland, E. Abouheif and J. Felsenstein for providing valuable and fruitful discussions about the comparative method. Some body mass data were supplied by N. Bernal, D. Bullock, M. Cano, H. Chen, G. Dubost, J.L. Galaz, J.A. Hart, M. Krasinska, S. Lovari, C. Packer, A. Rosser, M.R. Stanley Price and J.C. Torres-Mura. The software to estimate incisor protrusion was provided by A.W. Illius. Some information about the phylogeny was supplied by A. Balmford. R. Symonds helped to clarify the names of some species from the Cambridge Museum. The senior author would like to thank

G. Baillie for editing the first draft of the paper, and C. Nores from the Instituto de Recursos Naturales y Ordenación del Territorio for his support. This work received funding from Training and Mobility of Researchers of the European Communities and The Scottish Executive Rural Affairs Department.

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APPENDIX

Species	Male					Female					References
	M	MZW	OSA	IB	IP	M	MZW	OSA	IB	IP	
<i>Camelus dromedarius</i>	545.0	5.44	29.21			545.0	4.41	25.04			2, 44
<i>Lama guanicoe</i>	109.5	3.08	7.42			99.0	2.62	7.36			2, 9, 44
<i>Vicugna vicugna</i>	40.5	2.75	5.75			37.5	2.11	4.15			2, 9, 15, 44
<i>Hyemoschus aquaticus</i>	9.8	1.55	2.43			12.0	1.51	2.71			2, 8, 17, 44
<i>Tragulus meminna</i>	3.1	1.36	1.20	1.02	0.42	4.6	1.45	1.38	1.36	0.70	35, 44
<i>Tragulus javanicus</i>	1.3	1.21	0.94	0.98		1.5	1.14	1.09	1.00		3, 44
<i>Tragulus napu</i>	5.8	1.46	1.30	1.24	0.76	5.9	1.44	1.34	1.06	0.61	3, 44
<i>Giraffa camelopardalis</i>	1190.2	9.30	27.58	8.31	7.09	814.3	6.54	29.46	7.68	6.92	1, 6, 12, 17, 24, 32, 34, 44, 45, 49
<i>Okapia johnstoni</i>	200.0	5.37	21.57			200.0	5.03	18.57			2, 17
<i>Boselaphus tragocamelus</i>	253.3	4.96	12.84			136.3	4.85	14.10			2, 24, 44
<i>Tetracerus quadricornis</i>	18.0	2.20	3.40			17.0	1.97	3.46			2, 44
<i>Synceros caffer</i>	642.9	10.72	22.31			467.5	9.29	19.04			1, 6, 16, 17, 23, 24, 25, 26, 32, 34, 44
<i>Bubalus bubalis</i>	1200.0					800.0					24, 44
<i>Bubalus depressicornis</i>	156.0	4.24	6.08			145.0	4.08	6.78			2
<i>Bos gaurus</i>	848.4	9.69	23.08			701.9	8.03	19.84			24, 26, 37, 44
<i>Bos javanicus</i>	750.0	7.11	17.81			450.0	7.32	18.76			2, 44
<i>Bos taurus</i>	384.0					327.5					2, 44
<i>Bos grunniens</i>	590.5					306.0					24, 44
<i>Bison bison</i>	795.3	10.12	21.58			452.8	8.72	20.31			2, 24, 32, 44
<i>Bison bonasus</i>	718.0	9.86	19.61			423.0	7.26	16.24			24, 36
<i>Tragelaphus scriptus</i>	49.7	3.20	4.24	2.44	1.04	31.1	2.57	3.96	2.63	1.34	16, 17, 24, 26, 31, 32, 44, 45
<i>Tragelaphus angasi</i>	110.2	4.13	8.19	3.90	1.69	64.4	3.40	7.57	3.58	1.99	2, 17, 24, 26, 32, 44, 45
<i>Tragelaphus spekei</i>	102.3	3.75	6.25	3.17	1.53	60.2	2.97	6.43	2.94	1.76	2, 16, 17, 24, 44
<i>Tragelaphus imberbis</i>	95.6	4.14	8.38			62.1	3.36	8.04			1, 2, 16, 17, 23, 24, 32, 34, 44
<i>Tragelaphus strepsiceros</i>	240.8	5.49	14.09			159.2	4.84	13.70			2, 16, 17, 32, 34, 44, 45
<i>Tragelaphus buxtoni</i>	232.0	5.53	11.07			166.7	4.55	10.66			2, 17
<i>Tragelaphus oryx</i>	647.3					415.8					1, 2, 6, 16, 17, 21, 23, 24, 25, 26, 32, 34, 44

<i>Sylvicapra grimmia</i>	18.3	1.94	3.03	1.67	0.82	19.6	1.79	2.73	1.85	1.12	16, 17, 26, 32, 44, 45
<i>Cephalophus maxwelli</i>	6.5					7.2					2, 17, 44
<i>Cephalophus monticola</i>	4.4			1.15	0.52	5.1			1.12	0.44	2, 8, 17, 44, 45
<i>Cephalophus callipygus</i>	18.6					18.4					2, 8, 16, 17, 44
<i>Cephalophus dorsalis</i>	20.3	2.45	3.95			19.5	2.58	4.00			2, 8, 16, 17, 44
<i>Cephalophus jentinki</i>	70.3					80.5					2, 17
<i>Cephalophus leucogaster</i>	16.1			1.85	0.58	17.8			1.72	1.07	2, 8, 16, 17, 44
<i>Cephalophus natalensis</i>	13.1					12.1					2, 17, 32, 44
<i>Cephalophus niger</i>	19.9					18.4					2, 17, 44
<i>Cephalophus nigrifrons</i>	13.3					15.0					2, 8, 16, 17, 44
<i>Cephalophus ogilbyi</i>	20.4					22.5					2, 17, 44
<i>Cephalophus rufilatus</i>	10.1					10.3					2, 16, 17, 44
<i>Cephalophus spadix</i>	55.6	2.73	4.52			61.2	2.82	4.47			2, 16, 17
<i>Cephalophus sylvicultor</i>	52.5	3.67	8.87			72.0	3.56	8.20			2, 8, 16, 17, 44
<i>Cephalophus zebra</i>	13.9					14.7					2, 17
<i>Pelea capreolus</i>	24.0					25.0					2, 17, 32, 44
<i>Ourebia ourebi</i>	14.1			2.27	1.06	15.1			2.08	0.95	16, 17, 26, 32, 44, 45
<i>Oreotragus oreotragus</i>	11.3	1.45	2.36	1.36	0.79	13.0	1.48	2.33	1.48	0.76	16, 17, 26, 32, 44, 45
<i>Neotragus batesi</i>	2.4					2.8					2, 8, 16, 17, 44
<i>Neotragus moschatus</i>	4.8	1.23	1.29	1.25	0.52	5.1	1.10	1.25	1.22	0.52	2, 16, 17, 26, 32, 45
<i>Neotragus pygmaeus</i>	2.0	1.10	1.07			2.2	1.11	1.09			2, 17, 44
<i>Madoqua kirki</i>	4.6	0.60	1.29	1.15	0.70	5.1	0.63	1.33	1.03	0.72	2, 16, 17, 20, 21, 26, 32, 34, 44, 49
<i>Madoqua guentheri</i>	3.7	0.60	1.37	1.27	0.78	4.5	0.51	1.26	1.05	0.71	2, 16, 17, 18
<i>Madoqua saltiana</i>	2.3			1.02		2.6			1.01		2, 16, 17
<i>Raphiceros campestris</i>	10.9	1.35	1.88			11.3	1.39	1.87			16, 17, 32, 44, 45
<i>Raphiceros sharpei</i>	7.4			1.42		7.8			1.43		2, 16, 17, 44, 45
<i>Raphiceros melanotis</i>	10.7	1.36	1.79			10.5	1.38	1.90			17, 26, 44, 45
<i>Dorcotragus megalotis</i>	10.0	1.12	2.17			10.7	1.25	2.19			2, 17
<i>Saiga tatarica</i>	42.5	2.52	4.31			32.3	2.04	3.98			2, 24, 38, 44
<i>Litocranius walleri</i>	35.0	2.19	2.70	2.20		34.3	1.78	2.45	2.07		17, 23, 32, 44
<i>Anmodorcas darkei</i>	30.6	2.01	2.74	1.81	0.98	25.4	1.49	2.92	2.05	1.38	2, 17, 44
<i>Antilope cervicapra</i>	40.2	2.45	4.44			34.4	2.23	4.61			2, 26, 37, 44
<i>Antidorcas marsupialis</i>	40.7	2.20	4.05			35.5	1.93	3.95			2, 17, 32, 44, 45
<i>Procapra gutturosa</i>	31.5	3.32	5.69			24.0	2.95	4.74			2, 44, 46
<i>Gazella subgutturosa</i>	27.3					23.0					19, 44
<i>Gazella dama</i>	68.0					51.0					2, 17, 44
<i>Gazella soemmerringi</i>	45.4					33.6					2, 17

Appendix—continued

Species	Male					Female					References
	M	MZW	OSA	IB	IP	M	MZW	OSA	IB	IP	
<i>Gazella granti</i>	72.1	2.33	5.83			46.0	2.40	5.91			1, 2, 17, 21, 23, 25, 26, 32, 44
<i>Gazella gazella</i>	23.3					20.8					19, 38, 44
<i>Gazella dorcas</i>	16.3			1.79		13.3			1.92		2, 17, 19, 44
<i>Gazella leptoceros</i>	27.2			2.43	1.03	20.9			2.14	1.31	2, 17
<i>Gazella rufifrons</i>	27.0					20.7					2, 17, 44
<i>Gazella thomsoni</i>	22.7			2.55	1.35	17.8			2.22	1.15	2, 23, 26, 32, 34, 44
<i>Gazella spekei</i>	21.3	1.76	3.49			16.6	1.57	3.07			2
<i>Gazella cuvieri</i>	29.4			2.53		20.4			2.43		2, 17
<i>Redunca arundinum</i>	58.3	3.20	4.90	3.08	1.09	43.2	2.88	5.10	3.13	1.19	16, 17, 32, 44, 45
<i>Redunca fulvorufa</i>	30.1	2.50	3.70			28.5	2.43	3.57			2, 16, 17, 32, 44, 45
<i>Redunca redunca</i>	51.6					40.3					16, 17, 44
<i>Kobus ellipsiprymnus</i>	236.8	5.78	11.98	5.06	2.63	187.3	4.70	10.61	4.44	3.06	1, 2, 6, 17, 23, 25, 32, 34, 44, 47
<i>Kobus leche</i>	104.3	4.08	6.26			78.7	3.36	5.35			2, 16, 17, 24, 44, 45
<i>Kobus vardonii</i>	76.0	3.70	5.91			63.5	3.38	5.73			2, 16, 17, 32, 44, 45
<i>Kobus kob</i>	97.5	3.82	6.32			61.9	3.16	5.82			17, 23, 32, 44
<i>Addax nasomaculatus</i>	117.7	3.86	10.13			84.7	3.88	9.91			2, 17, 44
<i>Hippotragus equinus</i>	274.4	5.97	14.96			256.4	5.51	15.23			17, 24, 32, 44
<i>Hippotragus niger</i>	235.2	5.20	11.04	6.04	3.01	216.6	5.18	11.04	5.29	2.96	2, 17, 24, 26, 32, 44, 45
<i>Oryx gazella</i>	178.0	5.39	14.05			166.4	4.79	12.77			2, 17, 22, 23, 24, 26, 32, 34, 44, 45
<i>Oryx leucoryx</i>	85.9					80.1					2, 44
<i>Aepyceros melanopus</i>	56.9	3.31	5.74	3.34	1.73	43.8	2.92	5.47	3.03	1.43	2, 6, 14, 21, 23, 24, 32, 45
<i>Damaliscus hunteri</i>	91.0	4.69	8.26			86.0	4.50	8.53			2, 17, 44
<i>Damaliscus dorcas</i>	71.1	4.31	6.72			69.2	4.27	6.16			2, 17, 32, 44, 45
<i>Damaliscus lunatus</i>	137.0	5.38	7.64	5.42	2.56	120.1	5.30	8.67	5.29	3.06	17, 23, 24, 26, 32, 34, 44, 45, 49
<i>Alcelaphus buselaphus</i>	152.1	5.76	8.61			144.6	5.38	8.44			1, 6, 17, 23, 24, 25, 26, 32, 34, 44, 45, 49
<i>Alcelaphus lichtensteini</i>	178.3			6.45	3.12	162.7			5.89	2.94	34, 44, 45, 49
<i>Connochaetes gnou</i>	166.7					135.0					24, 26, 34, 44, 45
<i>Connochaetes taurinus</i>	235.3	6.57	11.49			184.9	6.03	11.48			17, 45
											1, 2, 17, 21, 23, 24, 25, 26, 32, 34, 44, 45, 49

Appendix—continued

Species	Male					Female					References
	M	MZW	OSA	IB	IP	M	MZW	OSA	IB	IP	
<i>Muntiacus reevesi</i>	14.7	2.22	2.90			11.8	2.10	3.01			3, 10, 44
<i>Muntiacus crinifrons</i>	23.1					24.1					43, 44
<i>Muntiacus muntjak</i>	20.9	2.48	3.95	1.99	1.01	15.1	2.49	4.23	1.93	1.00	3, 35, 44
<i>Axis porcinus</i>	44.1	2.64	4.80	3.33	1.98	30.6	2.59	4.86	2.54	1.28	2, 35, 44
<i>Cervus axis</i>	80.7			2.79	1.72	48.7			3.34	0.83	10, 32, 35, 37, 44
<i>Dama dama</i>	68.0	3.82	6.92			44.6	3.30	7.09			2, 10, 24, 44
<i>Elaphurus davidianus</i>	207.3	5.85	15.01			149.9	4.98	14.53			2, 10
<i>Cervus nippon</i>	56.5	3.15	5.68	7.31	0.04	37.4	2.79	5.36	2.79	1.65	2, 10, 44
<i>Cervus elaphus</i>	185.1					140.2					10, 17, 28, 44, 48
<i>Cervus canadensis</i>	335.0	7.75	18.49			252.0	6.48	17.65			10, 32
<i>Cervus eldi</i>	105.0					72.0					10, 44
<i>Cervus duvauceli</i>	223.1			4.28		142.0			4.16		10, 37, 44
<i>Cervus timorensis</i>	73.0					53.0					44
<i>Cervus unicolor</i>	206.3	5.45	13.95			131.8	4.73	13.51			2, 10, 33, 35, 37, 44

References: 1 = Astley-Maberly (1960), 2 = authors' unpublished data, 3 = Barrette (1982), 4 = Behrendt (1960), 5 = Bleich *et al.* (1997), 6 = Bourliere and Verschuren (1960), 7 = Bunnell and Olsen (1976), 8 = Fernández-Baca (1991), 9 = Geist and Bayer (1988), 10 = Gross *et al.* (1995), 11 = Hall-Martin (1977), 12 = Hamilton and Whitaker (1979), 13 = Hershkovitz (1982), 14 = Hofmann *et al.* (1983), 15 = Kingdon (1982), 16 = Kingdon (1997), 17 = Kingswood and Blank (1996), 18 = Kingswood and Kumamoto (1996), 19 = Kingswood and Kumamoto (1997), 20 = Lamprey (1964), 21 = Ledger (1964), 22 = Ledger (1968), 23 = MacDonald (1984), 24 = Meinertzhagen (1938), 25 = Meinertzhagen (1957), 26 = Miquelle *et al.* (1992), 27 = Mitchell *et al.* (1976), 28 = Novak (1991), 29 = O'Gara (1970), 30 = Odendaal (1977), 31 = Owen-Smith (1988), 32 = Pan (1991), 33 = Petersen and Casebeer (1971), 34 = Phillips (1980), 35 = Pucek (1986), 36 = Schaller (1967), 37 = Schaller (1977), 38 = Schaller and Junrang (1988), 39 = Schwartz *et al.* (1987), 40 = Seip and Bunnell (1984), 41 = Sempere *et al.* (1996), 42 = Sheng and Hogue (1980), 43 = Silva and Downing (1995), 44 = Smithers (1983), 45 = Sokolov and Lushchekina (1997), 46 = Spinage (1982), 47 = Staines (1980), 48 = Talbot and Talbot (1961), 49 = Weckerly and Nelson (1990).

Abbreviations: M = body mass (kg), MZW = muzzle width (cm), OSA = occlusal surface area (cm²), IB = incisor breadth (cm), IP = incisor protrusion (cm). See the Methods section for a detailed description of the variables.