

# Sexual Selection and Senescence: Male Size-Dimorphic Ungulates Evolved Relatively Smaller Molars than Females

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Submitted June 2, 2006; Accepted March 27, 2007;  
Electronically published July 19, 2007

Online enhancements: appendixes.

**ABSTRACT:** As a general rule, males of sexually dimorphic ungulate species have evolved larger body size than females but shorter reproductive life spans as elements of their strategy for intrasexual competition for mating opportunities. Evolutionary theories of senescence predict that the durability of somatic structures should relate to the length of reproductive life span. This prediction has recently been tested for red deer (*Cervus elaphus*): molariform teeth of males are smaller and less durable than those of females, which corresponds with sex differences in reproductive life span. However, general evidence that male teeth are smaller than expected by allometric rules as a consequence of sexual selection for increasing male body mass requires an interspecific comparison between dimorphic and nondimorphic ungulates. Here we investigate the relationship between cheek-teeth size (occlusal surface area; OSA) and body mass in 123 species of extant ungulates. We found lower slopes for dimorphic species compared with nondimorphic ones and smaller OSA, relative to body mass, in males of dimorphic species compared with females of dimorphic species. Rates of evolution of OSA relative to rates of evolution of body mass were greater in females than in males and also greater in nondimorphic than in dimorphic species. Our results are consistent with the hypothesis that sexual selection in polygynous male ungulates favors body size more than tooth size, with possible consequences in male senescence via early depletion of male teeth compared to females.

**Keywords:** senescence, sexual selection, sexual dimorphism, tooth wear, mating systems, mammalian herbivores.

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Am. Nat. 2007. Vol. 170, pp. 370–380. © 2007 by The University of Chicago. 0003-0147/2007/17003-41874\$15.00. All rights reserved.  
DOI: 10.1086/519852

Permanent teeth in many animals do not grow once fully emerged, and their crowns cannot be repaired when damaged or worn (Hillson 1986; Lucas 2004). These types of teeth are used throughout an animal's lifetime to comminute food up to the point when their crowns are fully eroded, so that at the time of eruption, teeth already have all their potential lifetime investment in repair and durability. Mastication is of paramount importance in the digestive processes of mammalian herbivores (Poppi et al. 1980; Pond et al. 1984; Pérez-Barbería and Gordon 1998). Reducing particle size through chewing increases the surface area on which symbiotic microorganisms can act, thereby increasing fermentation rate and cell wall degradation (McArthur and Sanson 1988; Pérez-Barbería and Gordon 1998). Tooth wear has been suggested to be a main proximal cause of senescence in ungulates because it can negatively affect body condition and individual performance (Tyler 1987; Skogland 1988; Gaillard et al. 1993; Ericsson and Wallin 2001; Loe et al. 2003).

Maximization of lifetime mating success in polygynous males normally involves the concentration of energy investment in a few highly successful reproductive seasons, thus leading to lower survival and reduced reproductive life span of males compared with those of females (Clutton-Brock 1988; Pemberton et al. 1992, 2004; Gaillard et al. 1993; Owen-Smith 1993; Loison et al. 1999a; Moore and Wilson 2002; Owens 2002).

When herbivorous ungulates radiated from woodlands into open grasslands, polygynous mating systems evolved, and as a consequence, sexual dimorphism in body size in favor of males arose (Jarman 1974; Janis 1982; Geist and Bayer 1988; Pérez-Barbería et al. 2002). Although sexual selection (Darwin 1871; Andersson 1994) is not the only process driving sexual size dimorphism (Isaac 2005), it appears that male-male contests for mating success are involved in most cases of sexual size dimorphism in ungulates (Clutton-Brock 1988; Reiss 1989; Owen-Smith

1993; Loison et al. 1999b; Pérez-Barbería et al. 2002). Teeth should increase in size in relation to body size if they are to maintain performance and durability (for discussions on scaling allometry of teeth size with body mass, see Fortelius 1985; Lucas 2004). However, if reproductive life span decreases by means other than teeth efficiency, as in male polygynous ungulates, tooth size and durability may not evolve at the same rate as body mass. Carranza et al. (2004) have recently shown that molariform teeth of male red deer are smaller than expected for their body mass. The consequences of smaller molars in males are a higher molar wear rate and earlier depletion compared with those of females (Loe et al. 2003; Carranza et al. 2004). The correlation between functional tooth duration, body condition, and reproductive life span in red deer indicates that the most likely cause of smaller molars in males is intrasexual selection for larger body size and shorter reproductive life span to maximize lifetime mating success (Clutton-Brock et al. 1982, 1988; Carranza et al. 2004). According to this interpretation, the relatively smaller size of molars found in red deer is expected to be a general pattern across polygynous ungulates in contrast to less polygynous species. Thus, we hypothesize that the size of molariform teeth relative to body size is expected to be smaller in dimorphic males than in females or nondimorphic males. Likewise, tooth size in males is expected to increase with body size across species but at a lower rate in males of dimorphic species.

## Material and Methods

### *Definitions of Variables and Data Collection*

The two main variables used were body mass and lower occlusal surface area (OSA), measured in 856 specimens of 123 species of the orders Proboscidea, Perissodactyla, Hyracoidea, and Artiodactyla, which make up 49% of the total extant *Ungulata* species (Nowak 1999). The number of specimens within species for which complete information was available ranged between 1 and 26 (females: range = 1–21, mean = 3.6; males: range = 1–26, mean = 3.7; see fig. 1 and appendix A in the online edition of the *American Naturalist* for details on the data sources). OSA was defined as the summation of the products of maximum width  $\times$  maximum length of the crown of each lower premolar and molar tooth of one side of the mandible ( $\text{cm}^2$ ). We used OSA in our analyses because (1) it is related to teeth durability and in turn to senescence, (2) it is not heavily affected by tooth wear, and (3) as far as we know, it was the variable for which the most comprehensive data set on ungulate species was already available. In order to provide analytical evidence that OSA correlates with a standard measurement of cheek teeth durability (degree

of hypsodonty; crown height), we explored the data set used by Carranza et al. (2004) for red deer. We selected only 2-year-old animals (66 females, 169 males) because at this age, tooth wear is negligible. We applied generalized linear models to account for differences in sample size between sexes, and we fitted a model in which the response variable was the crown height of the first lower molar ( $M_1$ ) and the fixed effects were OSA + sex + OSA  $\times$  sex. The model clearly indicated that OSA of the first molar is positively correlated with crown height (common slope for both sexes = 0.027, SE = 0.0046;  $F = 35.07$ ,  $df = 1, 231$ ,  $P < .001$ ) and that sex and OSA  $\times$  sex were not significant ( $F = 0.31$ ,  $df = 1, 231$ ,  $P = .581$ ;  $F = 2.05$ ,  $df = 1, 231$ ,  $P = .153$ , respectively) no matter in what order they were fitted in the model.

Tooth wear rate can be sex biased (Loe et al. 2003; Carranza et al. 2004), but OSA, as it was defined above, is a variable trait that is not affected much by tooth wear, since the maximum extent of premolars and molars in length and width is very close to the gum line and is therefore removed from the wearing effect caused by food abrasion during comminution. However, in order to ensure that the effect of wearing did not affect our results, we proceeded as follows. The OSA records were classified into seven arbitrary categories in relation to the degree of tooth wear on the occlusal surface of  $M_3$ , ranging from recently erupted and nonworn to heavily worn (C. Janis, personal communication). We ran a sensitivity analysis by applying the methods described in "Statistical Analysis" on the records of specimens that had nonworn to moderately worn  $M_3$  and compared the results with those of the same analysis applied to the records of specimens with heavier tooth wear than the previous wear class. The results from both analyses were consistent: the inclusion of specimens with marked tooth wear did not sex-bias the results. Consequently, in order to generalize our findings for the greater number of species as possible, we used all the available records in the analyses presented in this study.

Species were classified as dimorphic and nondimorphic in body mass to test our hypotheses, dimorphic species being those in which males were larger than females. Classifying species using this criterion can bias the number of species allocated to each class because of the fact that species with not much sexual dimorphism in body mass tend to be recorded as being exactly the same weight in the literature. In order to avoid this problem, we fixed three arbitrary categories of dimorphism based on three different thresholds: a strict threshold of males  $>$  females, males being 5% larger than females, and males being 10% larger than females. Analyses were run using these three thresholds of dimorphism, and the results obtained did not differ between the arbitrary threshold groups. However, in order to allow for a margin of error in the classification, we presented

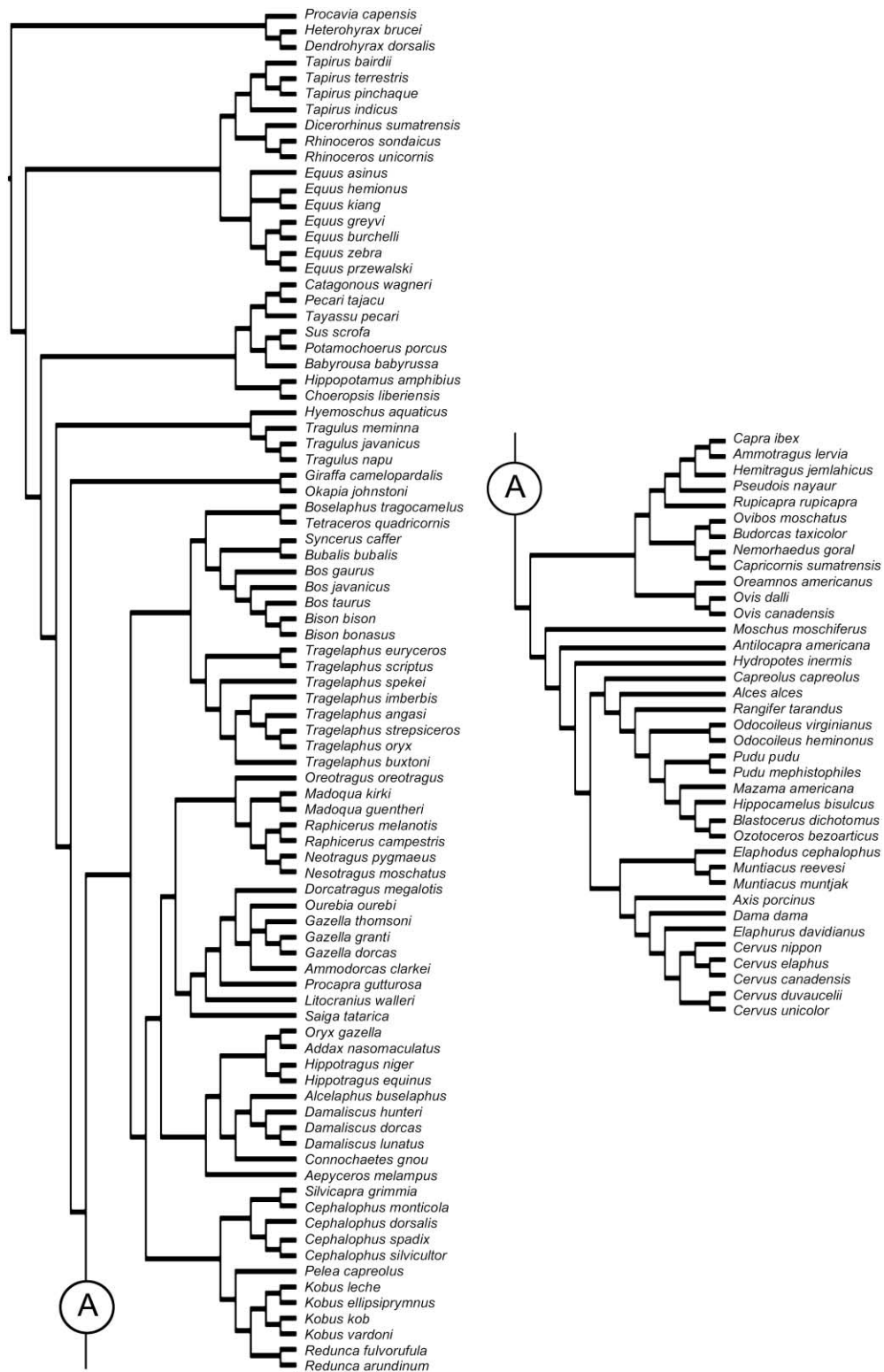


Figure 1: Phylogenetic relatedness of the species included in the study (branch lengths are arbitrary; see “Material and Methods”).

the analyses using a 5% sexual dimorphism threshold in body mass.

### Phylogenetic Information

The phylogeny used in this analysis comes mainly from Pérez-Barbería and Gordon (2001). It is a composite based on molecular studies (Gatesy et al. 1997; Randi et al. 2001) and morphological and paleontological information derived from a variety of sources (Kingdon 1982; Corbet and Hill 1986; Gentry and Hooker 1988; Janis and Scott 1988; Gentry 1992; Garland and Janis 1993; Nowak 1999). Polytomies in the phylogeny were resolved following Pérez-Barbería and Gordon (2001). None of these studies used information on body mass or OSA to construct the phylogenetic tree. Information on branch lengths was not available for all species in the phylogeny; therefore, we applied Pagel's algorithm (Pagel 1992) to estimate branch lengths using PDAP 5.0 software (Garland et al. 1992). We ran a sensitivity test on our model (see below) in order to verify whether the results were conditional on the branch lengths assigned to the phylogeny. This was done using an alternative algorithm to estimate branch lengths (Grafen 1989). Our analysis showed that the results did not depend on which algorithm was used; therefore, we presented the analyses carried out using Pagel's algorithm. The phylogenetic tree is shown in figure 1.

We estimated the rates of evolution of OSA and body mass in males and females as the absolute value of the difference between actual and ancestral values of the traits divided by path length. Ancestral trait values were estimated using the  $\alpha$  parameter of the computer program CONTINUOUS for the analysis of comparative data (Pagel 1997, 1999), which is the estimated value of the trait at the root of the phylogenetic tree.

### Statistical Analysis

We used the analytical methodology described by Pérez-Barbería et al. (2004) and Pérez-Barbería and Gordon (2005), which applies linear mixed models using the method of residual maximum likelihood (REML; Patterson and Thompson 1971) to account for different sources of variation present in the data set. The random effect was the phylogenetic relatedness between species, since phylogenetically related species are expected to have OSAs of similar size in comparison with less related species (Harvey and Pagel 1991; see appendix B in the online edition of the *American Naturalist* and Pérez-Barbería et al. 2004 for a detailed description of the procedure).

Body mass and OSA were  $\log_{10}$  transformed and centered around their respective means before being used in the analyses. A series of exploratory analyses, in which the

species effect was fitted in the REML model as a random effect but the phylogenetic relatedness between species was ignored, indicated that the three-way interaction body mass  $\times$  sex  $\times$  dimorphism explained a negligible amount of variation in OSA; it was consequently removed from the analysis. The fixed effects in the model were body mass, sex, dimorphism, and their two-way interactions, and the random effect was species. A categorical variable, polygyny, was tested in an exploratory analysis, but it was not significant when included together with body mass and sexual dimorphism, since most polygynous species of ungulates are both large and dimorphic in body mass (Pérez-Barbería et al. 2002), and it was therefore removed from the final analysis. Additionally, we tested for differences in evolution rates in OSA between sexes and dimorphic categories, using the design described above but replacing OSA and body mass with their respective evolution rates. Statistical analyses were performed using the GenStat 6 statistical package (GenStat 2002).

## Results

### Effects of Body Mass, Sex, and Dimorphism on OSA

There was clear evidence of a phylogenetic signal in our data set, which supported the inclusion of the effect of phylogenetic relatedness in the analysis. First, the covariance between species and phylogenetic similarity were related by the phylogenetic parameter  $q = 6.36$  (table 1), which indicates association between both. Second, the deviance test against the null hypothesis that species are not phylogenetically related (nominal  $q = 1 \times 10^6$  vs. the optimal  $q = 6.36$ ) was highly significant ( $\chi^2 = 22.06$ ,  $df = 1$ ,  $P = 2.64 \times 10^{-6}$ ). The estimated parameter for species effects and its associated standard errors are shown in table 1.

After controlling for phylogeny we found that OSA increased with body mass in both sexes for nondimorphic as well as dimorphic species. The shallowest slope was in dimorphic males (0.488), followed by dimorphic females (0.497), nondimorphic males (0.549), and nondimorphic

**Table 1:** Estimated values of parameters in the model for random variation

Parameter	Estimate	Standard error conditional on $q$
$\sigma_{sp}^2$	.0141	.00208
$\sigma^2$	.0023	.00012
$q$	6.36	...

Note: Equations for the model are  $\text{Var}(y_i) = \sigma_{sp}^2 + \sigma^2$ ,  $\text{Cov}(y_i, y_j) = G(i, j)^q \times \sigma_{sp}^2$ .  $\sigma_{sp}^2$  = variance component of the species effect;  $\sigma^2$  = residual variance;  $q$  defines the relationship between phylogenetic relatedness and covariance.

females (0.558; table 2; fig. 2). However, the only significant difference between slopes was that dimorphic species had a shallower slope than nondimorphic species (dimorphic vs. nondimorphic = 0.50–0.56; SED = 0.032). This indicates that for species of large body mass, males and females of dimorphic species have smaller OSA than nondimorphic species. However, for smaller species, the pattern was inverted. The significant interaction between body mass and sex was not significant if it was fitted after sex  $\times$  dimorphism (Wald = 1.79, df = 1,  $P = .185$ ). This was due to the strong association between body mass and dimorphism—large species tend to be dimorphic—that confounds the effects. In addition, the three-way interaction between body mass, sex, and dimorphism was not significant (see “Material and Methods”), which indicated that slopes did not significantly differ between the sexes. Consequently, we can compare intercepts between sexes within dimorphic classes because they are not conditional on the position in which the  $Y$ -axis is in relation to the  $X$ -axis. Dimorphic females had significantly larger OSA than dimorphic males relative to body mass throughout the whole range of body mass (values of the intercept centered on the mean: females = 0.0657, males = 0.0199; SED = 0.00525). This trend was the opposite in nondimorphic species: males had significantly larger OSA than females, although the difference was smaller than in dimorphic species (females = 0.0253, males = 0.03839; SED = 0.00652; fig. 2). The departure of the regression

lines from the cloud of data points is mainly a consequence of the phylogenetic relatedness between species.

The residual variance at the species level of the model was considerably reduced by the addition of sex (38%) and the interactions between sex and body mass (17%) and sex and dimorphism (16%; table 3). When dimorphism and the interaction between body mass and dimorphism were fitted in the model, there was an increase of variance (6% and 3%, respectively) at the level of species; this was due to a repartitioning of the residual variation (table 3).

The partitioning of the variance for the different effects in the phylogenetic model described above did not differ from those of the conventional model, with the exception of the contribution of dimorphism, which was not significant in the conventional model (Wald = 1.34,  $P = .248$ ; table 2). All the two-way interactions between body mass, sex, and dimorphism were significant, and also, as in the phylogenetic model, the interaction between body mass and sex was not significant if it was fitted after sex  $\times$  dimorphism (Wald = 2.57, df = 1,  $P = .109$ ). This indicates that the relationship between body mass and dimorphism is not greatly affected by the phylogenetic relationships between the species of our data set.

#### *Rates of Evolution of OSA and Body Mass*

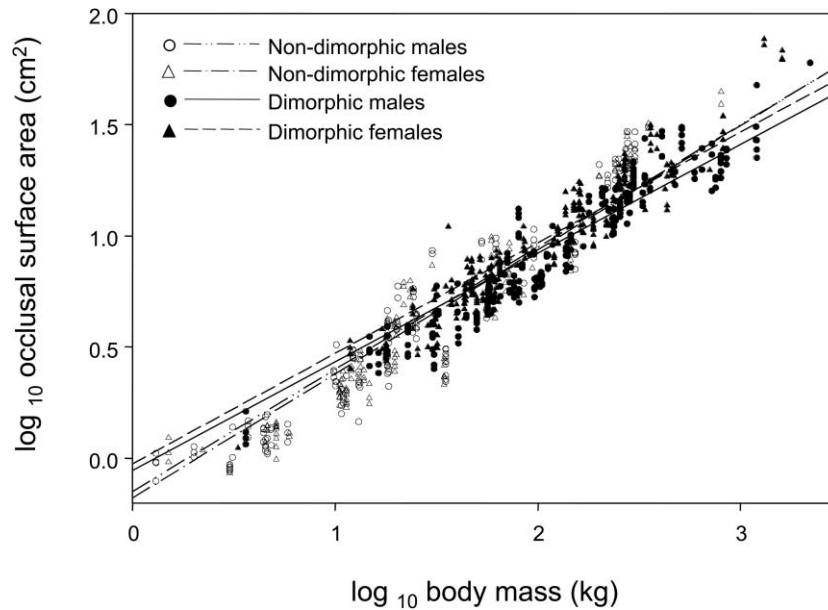
After accounting for the variability between species as a random effect (table 4, conventional model), the model

**Table 2:** Intercepts, slopes, and statistics of the residual maximum likelihood models of occlusal surface area against body mass, sex, and sexual dimorphism in body mass

Regression parameters estimate	Wald	df	$P$	Effect	Intercept	Slope
Conventional model:						
Log body mass	1715.74	1	<.001	Female, ND	.042 (.016)	.66 (.021)
Sex	62.11	1	<.001	Male, ND	.055 (.017)	.65 (.021)
Dimorphism	1.34	1	.248	Female, D	.013 (.012)	.53 (.022)
Log body mass $\times$ sex	39.23	1	<.001 <sup>a</sup>	Male, D	-.036 (.013)	.52 (.021)
Log body mass $\times$ dimorphism	34.71	1	<.001			
Sex $\times$ dimorphism	52.71	1	<.001			
Phylogenetic model:						
Log body mass	715.37	1	<.001	Female, ND	-.005 (.030)	.56 (.029)
Sex	37.30	1	<.001	Male, ND	.008 (.031)	.55 (.029)
Dimorphism	3.70	1	.054	Female, D	.035 (.027)	.50 (.022)
Log body mass $\times$ sex	25.19	1	<.001 <sup>a</sup>	Male, D	-.011 (.027)	.49 (.022)
Log body mass $\times$ dimorphism	6.58	1	.010			
Sex $\times$ dimorphism	44.80	1	<.001			

Note: In the conventional model, species are included as random variation but phylogenetic relatedness is not taken into account; residual variance ( $\sigma^2$ ) = 0.00229 (SE = 0.000121). In the phylogenetic model, relatedness between species is included in the model as a source of random variation;  $\sigma^2$  = 0.00226 (SE = 0.000120). The reference levels of sex and dimorphism effects are female and nondimorphic species, respectively. Body mass and occlusal surface area were centered to their respective mean values (164 kg and 9.78 cm<sup>2</sup>). Standard errors are given in parentheses. D = dimorphic species; ND = nondimorphic species.

<sup>a</sup> Effect is not significant when it is fitted after sex  $\times$  dimorphism (see “Results” for details).



**Figure 2:** Fitted values (regression line) of the residual maximum likelihood model of occlusal surface area against body mass after phylogenetic effect was controlled for. In the figure, both variables have been back transformed (i.e., they are  $\log_{10}$  transformed but not centered at their mean value) to improve clarity (see table 2 for details on the significance of the effects and their interactions). Equations are as follows: nondimorphic female,  $y = -0.178 + 0.558x$ ; nondimorphic male,  $y = -0.149 + 0.549x$ ; dimorphic female,  $y = -0.025 + 0.497x$ ; dimorphic male,  $y = -0.055 + 0.488x$ .

clearly indicates that the evolution rate in OSA was positively correlated with the evolution rate in body mass (common slope = 0.53,  $P < .001$ ). When we controlled for the evolution rate in body mass, the rate of change in OSA was greater in females than in males (females = 0.79, males = 0.75; SED = 0.015) and also greater in the nondimorphic species than in the dimorphic ones ( $P < .009$ ), independently of sex (sex  $\times$  dimorphism effect:  $P = .619$ ; table 4).

The analytical assessment of the phylogenetic independence indicates a very strong phylogenetic signal (deviance test against the null hypothesis of independent species: nominal  $q = 1 \times 10^6$  vs. the optimal  $q = 6.88$ ;  $\chi^2 = 23.36$ ,  $df = 1$ ,  $P = 1.34 \times 10^{-6}$ ). This suggests a strong link between the evolution rate of OSA across the phylogeny and the branching topology of the tree. After the phylogenetic relatedness between species was accounted for (table 4, phylogenetic model), the evolution rate of body mass still had a strong positive effect on the evolution rate of OSA (common slope = 0.47,  $P < .001$ ). Sex effect remained significant after evolution rate of body mass was accounted for ( $P = .037$ ), females showing a greater change in OSA in comparison with males (females = 0.21, males = 0.18; SED = 0.014).

Interestingly, the differences between nondimorphic and dimorphic species in the evolution rate of OSA disappeared after phylogeny was accounted for (nondimorphic =

0.21, dimorphic = 0.18; SED = 0.047), and no significant interactions between sex and dimorphism were detected by the model ( $P = .531$ ; table 4). These findings suggest that the rate of evolution of OSA in both sexes across the phylogenetic tree follows a pathway very similar to that of the evolution of dimorphism in body mass.

## Discussion

Our analyses reveal a general pattern of relatively small molariform teeth and slower evolutionary change of tooth size in dimorphic male ungulates compared with females, which is consistent with the hypothesis that sexual selection in polygynous males favors body size more than tooth size. The smaller OSA in male ungulates may be associated with shorter tooth longevity in males. This may not be so if the smaller OSA in dimorphic males could be compensated by increasing the degree of hypsodonty (highly crowned teeth) in males' molars compared to those of females. Data on crown height for individuals of known age (since crown height is heavily affected by tooth wear) are not available for most species. However, we found no evidence of differences between the sexes in the relationship between OSA and crown height in red deer (see "Material and Methods"), which suggests that the existence of a general pattern of OSA compensation by more hypsodont molars in dimorphic males is unlikely.

**Table 3:** Estimated variance components of the full model of table 2

Random term	Fixed-effect model					
	Log body mass	Log body mass + sex	Log body mass + sex + dimorphism	Log body mass + sex + log body mass × sex	Log body mass + sex + dimorphism + log body mass × dimorphism	Log body mass + sex + dimorphism + log body mass × sex + log body mass × dimorphism
$\sigma_{sp}^2$	.02979	.01844 (38.13)	.01954 (-5.98)	.01627 (16.72)	.01676 (-3.01)	.01413 (15.69)
$\sigma^2$	.00231	.00240 (-4.16)	.00237 (1.42)	.00237 (.11)	.00234 (1.17)	.00226 (3.17)

Note: Log body mass constitutes the base fixed model; additional effects are sequentially added to the base model. The sequential percentage of explained variance is given in parentheses. See table 1 for definitions of parameters.

Dimorphism was a more important effect than sex in explaining variance in the relationship between OSA and body mass. This could be because (1) male OSAs are expected to be relatively small among dimorphic species, and (2) species evolve more independently than sexes within species, so the traits of females should correlate with those of males of the same species (Lande 1980; Lande and Arnold 1985; Reeve and Fairbairn 2001; Badyaev 2002). In addition, the slopes of the relationship between body mass and OSA were similar in males and females of dimorphic species, and both slopes were shallower than those of nondimorphic species.

Males of dimorphic species consistently showed smaller OSAs than females throughout the whole range of species body mass, in support of the main prediction of the hypothesis. For nondimorphic species, however, we found slightly larger OSAs in males than in females. For red deer, Carranza et al. (2004) found that males wore their molars at a higher rate than expected from their smaller size with respect to females; they suggested that OSAs of males should be proportionately larger than those of females if they were selected to maintain durability. Possible causes for higher wear rate are lower-quality diet (i.e., more fibrous and therefore more abrasive) or processing disproportionately more food in order to achieve either rapid growth or high instantaneous performance during prime age (see, e.g., Yoccoz et al. 2002; Carranzana et al., forthcoming). Although our hypothesis does not predict larger molars in males of nondimorphic species compared with females, this finding adds relevance to the result of an opposite pattern in dimorphic species.

We found an unexpected interaction between body mass and dimorphism: OSAs of dimorphic ungulates were smaller than those of nondimorphic ones only for large species, not for small ones. This result could partially be explained in relation to the results on the rates of evolution. These imply that the relatively smaller OSAs re-

sulted after this trait failed to increase at the same rate as body size as evolution proceeded. Thus, it seems that the pattern found in large species requires an evolutionary process of increase in body size to emerge and it should not be expected in smaller species. However, why OSA tends to be even bigger in smaller dimorphic species compared with nondimorphic ones remains to be explained.

The main evolutionary implication of our results is that natural selection appeared to be unable to maintain the scaling of molar size when sexual selection produced an increase in body size in males. Reproductive success of female ungulates depends mainly on longevity (Clutton-Brock et al. 1982, 1988; Gaillard and Yoccoz 2003; Isaac 2005), whereas reproductive success of males is based mostly on mating opportunities resulting from direct male-male competition, especially in polygynous systems (Clutton-Brock et al. 1982, 1988; Gosling et al. 1987; Festa-Bianchet et al. 1990; Pemberton et al. 1992, 2004; Komers et al. 1994; Yoccoz et al. 2002; Isaac 2005). The fact that male reproductive success depends on winning fighting contests reduces the probability of reproduction beyond prime age. As a result, a common consequence of sexual selection based on male-male competition in ungulates is the shortening of reproductive life span of males relative to females (Clutton-Brock 1988; Andersson 1994; Loison et al. 1999a). Although information on reproductive life span of males and females in the wild is available for only a small number of species, reports on polygynous ungulates indicate that the reproductive life span of females is commonly twice that of males (e.g., Clutton-Brock et al. 1982, 1988; Jorgenson et al. 1997; Bérubé et al. 1999; Ericsson and Wallin 2001; Ericsson et al. 2001; McElligott et al. 2002; Weladji et al. 2002).

Shorter reproductive life span is expected to be related to reduced longevity (Rose 1984, 1991; Kirkwood and Austad 2000), and there is evidence for differential survival rates between the sexes in a number of species (Clutton-

**Table 4:** Regression parameters estimates, predicted means, and statistics of the residual maximum likelihood models on the evolutionary rate of occlusal surface area, controlling for the effect of evolutionary rate of body mass (ERBM), sex, and sexual dimorphism in body mass

	Regression parameters estimate and predicted			
	mean	Wald	df	P
Conventional model:				
Intercept	.85 (.034)			
ERBM	.53 (.023)	616.33	1	<.001
Sex		6.99	1	.008
Female	.79			
Male	.75			
Dimorphism		6.90	1	.009
Nondimorphic	.83			
Dimorphic	.72			
Sex × dimorphism		.25	1	.619
Female, ND	.85			
Female, D	.73			
Male, ND	.81			
Male, D	.70			
Phylogenetic model:				
Intercept	.23 (.068)			
ERBM	.47 (.026)	339.06	1	<.001
Sex		4.36	1	.037
Female	.21			
Male	.18			
Dimorphism		.57	1	.448
Nondimorphic	.21			
Dimorphic	.18			
Sex × dimorphism		.39	1	.531
Female, ND	.23			
Female, D	.19			
Male, ND	.19			
Male, D	.17			

Note: See table 2 for details on the conventional and phylogenetic models. Standard errors are given in parentheses. D = dimorphic; ND = nondimorphic.

Brock et al. 1982; Albon et al. 1983; Jorgenson et al. 1997; Bérubé et al. 1999; Loison et al. 1999a; Catchpole et al. 2000). However, the proximal causes of the relationship between short reproductive life span and reduced longevity are not so clear. Polygynous males may follow a risk-prone strategy compared to females (Clutton-Brock et al. 1982, 1988; Promislow and Harvey 1990; Promislow 1992), they are more susceptible to infectious diseases and parasites (Moore and Wilson 2002; Owens 2002; Wilson et al. 2004), and they allocate reproductive effort preferentially to prime age (Yoccoz et al. 2002), so that negative reproductive consequences after prime age are only weakly selected against (e.g., risk-prone behaviors, high testosterone levels, and reduced immunocompetence; Zuk and McKean 1996; Pelletier and Festa-Bianchet 2004). In addition, our results show that an important component of senescence in polygynous male ungulates may already be set up before

reproductive age by the production of teeth of relatively smaller size.

At least two evolutionary processes could explain the presence of smaller male teeth associated with the evolution of dimorphism. The first, related to the antagonistic pleiotropy hypothesis of senescence (Williams 1957; Hamilton 1966; Rose 1991), is selection for optimization of resources. In this case, teeth of males might be relatively smaller than those of females because males have to allocate more minerals into bones or antlers, which would produce reproductive benefits in early life despite having negative consequences (i.e., tooth depletion) in later life. However, the amount of material invested in slightly larger permanent and nonreparable teeth seems negligible compared with the amount of material invested in skeleton or in yearly deciduous antlers in cervids. Another possible explanation, also related to antagonistic pleiotropy, is that



teeth might have to be smaller in males in order to erupt earlier and allow rapid body growth. However, again, smaller teeth for earlier eruption seems to be an unlikely explanation because, for example, in red deer, first mandibular molars are functional before weaning in both sexes (Loe et al. 2003), and other molars appear to erupt even later in males than in females despite their relatively smaller size (Carranza et al. 2004).

If the benefits of producing smaller teeth are negligible, then the most likely explanation is that selection could be unable to increase the durability of somatic structures when there is no reproductive return. This second possible process simply means the lack of selection for larger teeth when male body size is selected for. Our results on evolution rates indicate that molar teeth have not been reduced in size with respect to females but have been simply "left behind" during the evolution of larger body size in dimorphic males. The disposable-soma hypothesis of senescence (Kirkwood 1985; Kirkwood and Rose 1991; Kirkwood and Austad 2000) predicts low rates of repair and less durable somatic structures when there is little reproductive return. Therefore, our findings for ungulate teeth may be regarded as being related to the disposable-soma hypothesis of senescence, as interpreted by Carranza et al. (2004), representing a particular case for which producing larger, more durable teeth would involve very little cost but also too little benefit to be selected for.

#### Acknowledgments

We thank C. Janis for allowing us to use her comprehensive data set on tooth measurements, D. Elston for writing the phylogenetic REML program, and J. Potts and C. Mateos for their statistical advice. G. Iason, O. Jones, and three anonymous referees provided constructive comments on the manuscript. The Scottish Executive Environment and Rural Affairs Department funded the research of F.J.P.-B. The Ministry of Educación y Ciencia of Spain contributed partially by projects REN2001-1524 and CGL2004-05993/BOS.

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