Sex-specific strategies of dentine depletion in red deer

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Abstract

Worn teeth in herbivore ungulates may be related to lower efficiency in mastication and hence lower performance. However, selection should favour maximal performance in terms of body mass and reproductive capacity during reproductive lifespan, when permanent teeth are already partially worn. We hypothesize that wear rate may respond to a strategy of use of tooth materials (notably dentine), which balances instantaneous wear rate and performance against tooth preservation for future performance and reproduction. In the present study, we investigated 4151 carcasses of Iberian red deer *Cervus elaphus hispanicus* and show that more worn molars were not related to lower performance throughout age. By comparing between sexes, tooth wear rates were smaller in females than in males, but the relationship between tooth wear and body performance also differed between the sexes: females did not show a significant relationship between tooth wear and performance but males with more worn teeth were in general heavier and had larger antlers until senile age, when more depleted teeth were related to smaller antlers. These results reveal, for the first time, sex-specific lifetime strategies of dentine expenditure: maintenance of performance ability throughout a longer reproductive lifespan in females, compared with maximizing current performance by depleting dentine reserves within a shorter lifespan in males.

Keywords: *Cervus elaphus*, life history, senescence, sexual selection, teeth

INTRODUCTION

Mastication is of central importance for herbivore mammals to obtain nutrients from ingested forage (Poppi et al., 1980; Pond, Ellis & Akin, 1984; PérezBarbería & Gordon, 1998a). Reducing particle size through chewing produces an increase in the surface area to which symbiotic microorganisms can act, thereby increasing fermentation rate and cell wall degradation (McArthur & Sanson, 1988; PérezBarbería & Gordon, 1998a). Ruminants have evolved an extreme comminution strategy, based on spending up to 12 h per day in chewing both at initial ingestion and rumination (Gordon & McAllister, 1970; Murphy et al., 1983; Semiadi et al., 1994).

Cheek-teeth morphology affects comminution efficiency (Pérez-Barbería & Gordon, 1998a) and changes with tooth wear, so that worn molar teeth may be less efficient in mastication (Severinghaus, 1949), thus reducing the nutritional use of ingested forage (Dean, Thorne & Moore, 1980). Tooth wear has been cited as proximal cause of senescence in ungulates as far as it can negatively affect body condition and performance (Tyler, 1987; Skogland, 1988; Gaillard et al., 1993; Ericsson & Wallin, 2001; Loe et al., 2003). However, the relationship between tooth wear and performance is not well understood. Tooth wear has been shown to be related to lower body weight in reindeer (Rangifer tarandus; Skogland, 1988; Kojola et al., 1998) and in red deer (Loe et al., 2003), although these relationships are questionable as they may have resulted from the correlation between initial molar height and body size (Mysterud et al., 2001; Loe et al., 2003). Some studies have reported that forage after mastication results in a larger particle size when teeth are more worn (red deer: Pérez-Barbería & Gordon, 1998b; koalas: Logan & Sanson, 2002). Experimental work with a group of red deer hinds showed some compensation of reduced comminution efficiency by increased chewing time, although only partially (Pérez-Barbería & Gordon, 1998b).

Although it is clear that completely worn molars are unlikely to adequately chew the forage, this does not necessarily mean that the gradual lost of dentine thickness is associated with a gradual loss of efficiency and performance. Rather, there may be a minimum height of molar crown to allow efficient comminution, and from which further wear would produce decreased performance and senescence. For example, the main relationship between tooth wear and reduced body weight in reindeer was found for the oldest females (aged between 11 and 14 years old; Kojola et al., 1998). It has been suggested that tooth effectiveness with respect to wear may follow a convex relationship, with an upper limit at some optimum degree of wear and decreasing thereafter (Lanyon & Sanson, 1986; McArthur & Sanson, 1988; PérezBarbería & Gordon, 1998a).

Maximum performance in ungulates is expected during prime age (Caughley, 1966; Clutton-Brock, Albon & Guinness, 1988), after several years of body growth and tooth wear. Selection is expected to penalize any wear pattern that reduces the efficiency for performance at the reproductive age. Therefore, from an evolutionary perspective, we may not expect a clear reduction in tooth efficiency until senile age. On the other hand, since teeth lose material as a function of the amount of friction with food, other things being equal, we may expect individuals processing comparatively higher amounts of food to achieve higher body performance but, at the same time, to experience higher tooth wear. This association would predict a positive, rather than a negative relationship between tooth wear and performance when other variables are controlled.

In the red deer (*Cervus elaphus*), tooth wear rates are higher for males than for females and are related to longevity in both sexes (Loe et al., 2003; Carranza et al., 2004). Sex-specific rates of tooth wear may be related to the use of different types of food (Fandos, Orueta & Aranda, 1993; Van Deelen, Anchor & Etter, 2000; Ericsson & Wallin, 2001). Red deer males may eat a lower-quality, more fibrous diet than females associated with sexual segregation (Clutton-Brock, Guinness & Albon, 1982; Staines, Crisp & Parish, 1982; Clutton-Brock, Iason & Guinness, 1987; Clutton-Brock & Albon, 1989; Conradt, Clutton-Brock &Thomson, 1999; Conradt, 1999; Barboza & Bowyer, 2000; Focardi et al., 2003). Also, male red deer should eat a higher amount of food than females due to their larger size (Mitchell, McCowan & Nicholson, 1976; Reiss, 1989), and an even higher amount if they select a lower quality diet (Bell, 1971; Geist, 1974; Jarman, 1974; Barboza & Bowyer, 2000). However, the way in which the rate of tooth wear affects performance in males and females is not well understood, nor whether the strategy of depleting tooth materials may also show sex-specific variations throughout life. Since permanent teeth in many animals, including the Cervidae, cannot be repaired in their external dimensions once fully emerged, molar crown height (notably dentine thickness) can be seen as a reservoir of material to be used when the animal needs to process food. Therefore, expenditure of limited dentine reserves throughout life may be understood as an evolved strategy that may also differ between the sexes.

It has been already shown that red deer males experience a more rapid increase of body mass until prime age and also wear their teeth at a higher rate than females (Carranza et al., 2004). Although a higher wear rate is expected for males compared with females due to the relatively smaller size of male teeth, tooth wear in males appears to be even higher than expected from sex differences in body weight and teeth size (Carranza et al., 2004). In the present study, we analyse tooth wear in male and female red deer harvested in hunts in South-western Spain between 1998 and 2006. The objective was to investigate the patterns of tooth wear in males and females with age and their relationship with other traits, such as body weight, fertility of females, and antler size of males, which can be taken as measures of performance ability (Clutton-Brock et al., 1982; Kruuk et al., 2002). The starting hypotheses were: (1) the pattern of tooth wear throughout life is expected to differ between the sexes as a component of a lifetime strategy of optimizing performance and reproduction and (2) more worn teeth relative to age are not expected to be related to lower performance, and even the opposite relationship is likely, although rapid tooth depletion may entail costs later in life.

MATERIAL AND METHODS

STUDY AREA AND RED DEER POPULATION

Animals used in the study were 2847 males (aged 2–12 years) and 1304 females (aged 2–18 years; see Appendix), harvested during hunting activities in naturally-occurring populations of Iberian red deer (*Cervus elaphus hispanicus*) in South-western Spain. In this area, deer feed mostly on natural pasture and Mediterranean shrub plants (*Phyllirea; Arbutus; Erica; Cistus*; Rodríguez-Berrocal, 1993), although it is quite common that managers provide some supplementary food (hay, alfalfa) during 1 or 2 months between late summer and early autumn (SánchezPrieto, Carranza & Pulido, 2004), which is the limiting season for red deer in this latitude (Carranza et al., 1991; Rodríguez-Berrocal, 1993; Carranza, 1999; Bugahlo & Milne, 2003). Thousands of red deer stags are hunted every year in the Spanish commercial hunt called Monteria. In this type of hunt, packs of dogs are released within a shrub area to move the deer outwards to the sites where hunters are placed. Normally, every male deer aged 2 years or older can be legally shot, hence the lack of 1-year-old males. For females, there are usually other noncommercial, management hunts aimed at reducing density. We took female samples from hunting actions that, in practice, are similar to a Monteria, where every female can be culled of any age, including calves, in a nonselective beating. As for males, we included females that were at least 2 years old in the analyses because, below this age, most of them are not yet reproducing due to causes other than tooth wear, which is actually not appreciable at this age. The hunting pressure on males is basically regulated by allowing only one Monteria per year in the same area and a minimum distance between hunters. For females, annual quotas are authorized by local government. Monteria has been proved to be a good method for obtaining unbiased samples (Martínez et al., 2005). In no case did our work lead to the shooting of additional deer (for examples of use of harvesting data, see Mysterud et al., 2001; Bonenfant et al., 2003; Loe et al., 2003; Carranza et al., 2004).

Data were collected throughout nine hunting seasons (from 1998 to 2006), usually from October to February. In the two first seasons, we collected only males (246 in total) and both males and females in the seven remaining seasons (2601 males and 1304 females). In every season, we usually collected twice as many males than females because hunting actions on males were much more common. The proportion of males and females was similar for the three metapopulations included in the study area (Monfragüe, Sierra de San Pedro, and Sierra Morena). Although there may be differences between years or populations in tooth wear patterns, we did not intend to investigate these effects. However, we performed explorative analyses (not shown), splitting up our data base under different criteria such as years, populations, habitat quality, population structure, supplementary feeding, or types of management, to guarantee that the general patterns presented here were not the result of the cross-sectional analysis of contrasting patterns.

DATA RECORDING

Field data

Each hunting day, we visited the location where culled animals were gathered. For each animal, we recorded a number of measurements in the field, and removed the mandibles for further laboratory analyses. In the field, we recorded body weight of the complete animal, between 1–3 h after death and using an electronic scale, to the nearest 0.5 kg. Males were always weighed before evisceration. When possible, females were weighed both before and after evisceration. Lean carcass weight of females was used for analyses when the reproductive status was a dependent variable, to exclude the weight of the reproductive tract and foetus. For analyses where body weight was related to tooth wear and for comparison with male body weight, we used the complete body weight of females. When females were only weighed after evisceration, we estimated the complete body weight by fitting them into a polynomial regression of live weight on carcass weight. The reproductive status of females was registered by inspecting the ovaries and uterus.

For males, the following antler measurements were made:

1. Antler length: beam length from burr excrecences to the most distant tip following external shape, averaged for both antlers.
2. Antler width (three variables): we measured perimeters of both antler beams at three points (1, burr; 2, base, below the brow-tine; and 3, at thinner portion between the bez-tine and the central, trez-tine) and then averaged each of them for both antlers.
3. Antler tines: total number of tines ≥ 2 cm long from both antlers.

It was not possible to take all the measurements for all individuals, so sample sizes for some measurements are below the total number of animals recorded and are variable among measurements. For some hunting actions on stags, we only had access to the heads, and not whole bodies, which produced differences between sample sizes for antler and body measurements.

Laboratory data

Age was estimated by counting cementum growth marks at the interradicular pad under the first molar (Mitchell, 1967) and checked by eruption patterns in younger animals. Ages are expressed in completed years from birth, so an animal aged N is living its N+1year of life, as used for humans.

Tooth wear was estimated from the crown height of the first molar (M1), which was measured, with a calliper by transverse cross-section of the M1 between its mesial and distal halves, as the distance (mm) from the lowest point at mid-crown down to the central peak where the dentine touches the cementum layers. The most commonly used index of tooth wear is the external crown height of the M1 measured as the distance from the distobucal cusp to the enamel–dentine line (Skogland, 1988; Fandos et al., 1993; Kojola et al., 1998; Ericsson & Wallin, 2001; Loe et al., 2003). However, external crown height to the cusp has two problems. One of them is that the enamel–cementum line may be difficult to accurately delimitate in some cases, or it may be affected by the degree of emergence of the tooth. Dentine thickness as measured by sectioning the whole tooth is not affected by the degree of emergence, which may be especially relevant for measurement in young animals. Also, molar wear in ruminants should be more intense in the centre of the crown than in the external cusps (Pérez-Barbería & Gordon, 1998a, b), producing a concave shape of the M1 occlusal surface. Indeed, in our data (males and females pooled), internal dentine thickness depleted at 12.7 years whereas external crown height did so at 15.6 years. When there was already no dentine at all at the centre of the M1 occlusal surface, the height of peripheral crown was still 2.7 mm on average. Although both measures were highly intercorrelated (R2 = 0.82; N=678), the relationship with age was stronger for internal crown height (R2 = 0.67; N = 678) than for external crown height (R2 = 0.60; N = 678). Therefore, as in Carranza et al. (2004), we preferred to use internal crown height as a more accurate estimation of dentine depletion at the central area of the occlusal surface. Hereafter, we will use crown height to refer to internal dentine thickness unless otherwise stated.

STATISTICAL ANALYSES

To test the relationship between crown height and age for males and females, we conducted a generalized linear model (GLM) analysis with crown height as the dependent variable, and sex and age as independent ones. We also included the quadratic value of age as independent variable because crown height followed a quadratic relationship with age (Loe et al., 2003; Carranza et al., 2004). The final model included the effect of independent factors and significant interactions.

Performance variables were body mass for both sexes (as it is known to be the main determinant of reproductive success in red deer; Clutton-Brock et al., 1988), together with reproductive status (pregnant or not) for females and antler size for males. Body mass may change within any hunting season as the animals recover after the rut. Therefore, we included the date of shooting as a covariate with body mass. For antler size, instead of analysing every antler trait separately, we entered the five antler variables described above into a principal components analysis. Most traits were correlated with each other so that the analysis grouped the variables into just one factor, which explained 84% of the variance. Values of the variable antler size were the scores for each individual extracted from the principal component factor.

To explore the relationship between crown height and body mass in males and females, we conducted a GLM analysis with body mass as dependent variable, sex as fixed factor, and crown height as the independent. The date of shooting and individuals' age were also introduced in the model as control covariates. The date of shooting was considered as an ordinal variable ranging from 1 for the first month of shooting (October) until the last one (February for males and April for females). Body mass followed a quadratic relationship with age (Carranza et al., 2004); thus, we fitted an orthogonal polynomial term on the GLM by adding the quadratic value of age as independent variable and centring the data prior to applying the quadratic transformation. Type III sum of squares was used in the analysis.

To test whether the relationship between body mass and crown height changed across lifespan, we added the interaction term between age (and its quadratic) and crown height, and a further interaction term with sex, age, and crown height to test whether the lifespan dependence of body mass–crown height relationship varied between the sexes.

The relationship between antler size and age was also quadratic (y=-2.36 + 0.923x-0.056x2; R2 = 0.573; F2,2231 = 1498.55; P < 0.001). Thus, to test the relationship between crown height and antler size in males and their variation across lifespan, we conducted another GLM analysis with centred-age and quadratic centred-age as control variables.

Crown height and age (the independent and a control variables when exploring the effects on performance) were highly correlated between them, but the values obtained in the colinearity diagnostic were between 0.26 and 0.24 for Tolerance and 3.82–4.11 for the Variance–Inflaction factor in males and females, respectively.

To visualize the effect of age on the relationship between crown height and performance variables (body mass or antler size), we made graphic representations of the parameter estimates (slopes) and their standard deviations for the relationship between crown height and performance (body mass or antler size) for each age class.

Finally, to test the relationship between crown height and reproductive status in females, we used a Logistic regression model on the variable ‘pregnant or not’. For this analysis, we removed all females culled in October because its reproductive status was still uncertain at this time. We used lean carcass mass, instead of total body mass, in the analysis of female reproductive status.

RESULTS

Tooth wear showed a decelerating pattern throughout life for both sexes but males wore their teeth faster than females (GLM with crown height as dependent variable, and sex, age, and quadratic age as independent ones: factor age^2: $F_{1,3309} = 119.036$, $P < 0.001$; sex–age interaction: $F_{1,3309} = 55.004$; males versus females: parameter estimates ± SE = -0.194 ± 0.026, $t = -7.416$, $P < 0.001$; the interaction sex × age^2 was not significant and hence removed from the model; Fig. 1).

The relationship between dentine and performance differed between sexes: the relationship between crown height and body mass, controlling for age and date of shooting was different for males and females (GLM results are shown in Tables 1, 2). For males, crown height was negatively associated with body mass (parameter estimates ± SE = -5.001 ± 0.742, $t = -6.741$, $P < 0.001$) whereas, for females, this relationship was nonsignificant (parameter estimates ± SE = -0.390 ± 0.483, $t = -0.807$, P = not significant). Furthermore, the interaction between age and crown height was significant, and so was the interaction between sex, age, and crown height (Table 1), demonstrating that the age-dependence of the body mass–tooth wear relationship varied between the sexes. Most males with more worn teeth had a higher body mass (negative relationship between body mass and crown height) except for those aged 7–9 years (Fig. 2A). For females, although the relationship between crown height and body mass was not significant (Table 2), there was a significant interaction between crown height and age (Table 2) because the relationship between crown height and body mass tended to shift from positive to negative thoughout life (Fig. 2B).

As for body mass, antlers were bigger in those males with lower crown height (more worn teeth) (GLM results are shown in Table 3; relationship between crown height and antler size after controlling for age and its quadratic term: parameter estimate ± SE = -0.158 ± 0.026, $t = -6.099$, $P < 0.001$). The effect of the interaction between age and crown height on antler size was also significant (Table 3). Until the end of reproductive age, males with higher tooth wear had a higher performance (antler size), whereas the relationship reversed for old males that showed a smaller antler size when they had more worn teeth (Fig. 3).

Reproductive status of females (pregnant or not) from 2–18 years of age did not depend on the degree of tooth wear, but only on body mass, and this appears to be the case for all female ages (logistic regression for pregnant or not, with M1 crown height as independent variable and age, date of shooting, and lean carcass weight as control variables: total likelihood ratio: $\chi^2 = 81.248$, d.f. = 7, $N = 740$, $P < 0.0001$; $R^2 = 0.120$; lean carcass weight: $\chi^2 = 53.107$, d.f. = 1, $P < 0.0001$; crown height: $\chi^2 = 2.473$, d.f. = 1, $P = 0.116$; date of shooting: $\chi^2 = 2.521$, d.f. = 1, $P = 0.112$; age: $\chi^2 = 2.097$, d.f. = 1, $P = 0.147$; age^2: $\chi^2 = 3.058$, d.f. = 1, $P = 0.080$; age × crown height: $\chi^2 = 2.299$, d.f. = 1, $P = 0.130$; age^2 × crown height: $\chi^2 = 1.713$, d.f. = 1, $P = 0.190$; deviance residuals goodness-of-fit tests: not significant).

DISCUSSION

The results of our study are in agreement with the previously reported pattern of decelerating tooth wear throughout life, which is faster in males than in females (Loe et al., 2003; Carranza et al., 2004). However, contrary to the widely accepted point that tooth wear should be related to lower performance (Tyler, 1987; Skogland, 1988; Gaillard et al., 1993; Ericsson & Wallin, 2001; Loe et al., 2003), our results show that more worn teeth relative to age were not generally related to a reduction of body mass, antler size, or fecundity. For females, we only found a weak tendency for more worn teeth to be related to lower body mass, which changed for the oldest ages. Female reproduction (pregnancy) did not appear to depend on tooth wear, but only on body mass. For males, higher performance in body mass and antler size was clearly related to more worn teeth until old age. The oldest males (> 9 years) with more depleted teeth still showed a higher body mass but smaller antlers, suggesting that the lower efficiency of depleted teeth in late life affects antlers more than body mass.

Prime age males (7–9 years old) were an exception to the generally negative relationship between molar height and body mass. We think, however, that this result is simply a consequence of the time when we weighed the animals. The hunting season begins every year in October, after the summer and after the rutting period of September. Summer is a shortage season in our study area (Carranza et al., 1991; Rodríguez-Berrocal, 1993; Carranza, 1999; Bugahlo & Milne, 2003), so all animals may show an increase in body mass as the autumn progresses, which is the reason why we included the date of shooting as a control variable. During the rut, however, weight loss does not affect all age-sex classes equally. It is well documented that rutting prime-age stags lose their body mass more than other age-classes (Yoccoz et al., 2002), which is a result of their low intake rate at that time coupled with their involvement in costly reproductive behaviours (e.g. harem holding; Clutton-Brock et al., 1982). Antler size, in turn, cannot be affected by the effort during the rut, and our results show that prime-age males with more worn teeth bore larger antlers. These same males may have participated more actively in reproduction, resulting in a higher weight loss, and thus producing a positive relationship between molar height and body mass when we weighed them after the rut.

Our data for each age-class belong to different individuals. The use of transversal data to infer patterns throughout lifetime is common in studies with longlived species such as ungulates (Mysterud et al., 2001; Bonenfant et al., 2003; Loe et al., 2003; Carranza et al., 2004). Transversal data might not represent patterns of change throughout lifetime if data for different ages were unbalanced with respect to any variable affecting the measured traits. For example, the average quality of sampled specimens may increase with age due to the higher survival of high-quality individuals. Although it is difficult to completely overcome this potential problem, our main results on the relationship between tooth wear and performance are based upon comparisons among individuals within age classes, which cannot be affected by age-related bias.

Why did males and females show different relationships between tooth wear and performance? The main features of molariform teeth commonly related to chewing effectiveness are the occlusal surface area, the contact area of molars during occlusion, and the length of the enamel cutting edges of the occlusal surface (Pérez-Barbería & Gordon, 1998a). Some of these properties change throughout life as teeth are used and worn down. Two main processes cause tooth wear: attrition with other dental pieces and friction with ingested materials. Either or both of these processes can affect some of the properties that influence comminution, but there is no consensus on how they do this. Enamel cutting edges (infoldings and infundibuli) of selenodont occlusal surfaces may work like blades so that attrition might contribute to maintain the tridimensional shape of the surface whereas both friction and attrition would tend to progressively reduce the height of the molar crown. Our results for females suggest some loss of effectiveness as the occlusal surfaces flatten down, although this is weakly related to performance during reproductive ages.

It is known that animals can compensate to maintain performance when teeth are becoming less effective. Experimental work with female red deer by Pérez-Barbería & Gordon (1998b) showed that the main mechanism used to compensate for reduced tooth effectiveness was intake modification and increasing investment in chewing behaviour during eating, although the compensation achieved by the group of females under study was only partial. Our findings of a weak positive relationship between molar height and performance throughout reproductive life for females are in agreement with their results. Why were females not able to fully compensate for the decreased effectiveness of their teeth? One interpretation is that increasing chewing behaviour would lead to increased tooth wear and a reduction of tooth durability. If females were to maintain current performance, they would deplete their teeth more rapidly, with potential associated costs in terms of late reproductive success and survival. This suggests a trade-off between maximizing short-term performance and maintaining duration of performance ability. Ungulate females appear to have been selected to favour survival rather than current performance (Gaillard & Yoccoz, 2003). Our data indicate that the female strategy in red deer tends to favour teeth durability rather than short-term performance compared with the strategy of males. At oldest ages, however, females also tended to converge to a 'male' strategy of a negative relationship between molar height and body mass. Indeed, our sample size for oldest females is small, but the significant shift throughout lifetime in the sign of the relationship between molar height and body mass suggests that the solution in the trade-off between current performance and maintenance may change from young to old females, resembling a 'terminal investment' pattern (Clutton-Brock, 1984).

Males, in turn, achieved higher levels of short-term performance throughout life by wearing their teeth, despite the fact that this strategy leads to a higher wear rate and early tooth depletion. This result is consistent with the 'mating strategy-effort' hypothesis (Yoccoz et al., 2002), which predicts that reproductive effort peaks in prime-aged males. The pattern found for males of predominately negative relationships between molar height and performance was completely unexpected in previous studies, and is consistent with the hypothesis that selection will maximize performance at the expense of tooth durability.

Sexual selection theory predicts a lower reproductive lifespan in polygynous males compared with females if male reproductive success is based on strong male–male competition over mates (Andersson, 1994) as in polygynous, dimorphic mammals (Ralls, Brownwell & Ballou, 1980; Promislow, 1992). According to this, evolutionary theories of senescence predict lower survival in polygynous males provided that their chances for reproduction are more steeply reduced after prime age compared with females (Haldane, 1941; Medawar, 1946; Hamilton, 1966). Sex differences in longevity in favour to females have been consistently reported for red deer (Clutton-Brock et al., 1982; Clutton-Brock et al., 1988; Mysterud et al., 2001; Loe et al., 2003; Carranza et al., 2004). Loison et al. (1999) questioned whether the shortening of male reproductive lifespan compared with females is the result of costs incurred during reproduction or whether it is the consequence of a different strategy of allocation of reproductive effort throughout lifetime. Our results of elevated tooth wear in males even before reproductive age support the latter explanation.

Evolutionary theories of senescence, and in particular the disposable-soma hypothesis (Kirkwood & Rose, 1991; Kirkwood & Austad, 2000), predict different solutions for the trade-off between current expenditure of somatic structures and bodily maintenance for future reproduction when reproductive lifespan differs due to causes other than body repair, as is the case for red deer (Carranza et al., 2004). We have already found that cheek-teeth in male red deer (Carranza et al., 2004), as well as in other male dimorphic ungulates (Carranza & Pérez-Barbería, 2007), are smaller than expected simply to maintain a similar workload compared with females. Furthermore, male teeth are highly under-provisioned if we take into account the processes that enhance differences in the wear rate between sexes, such as (1) differences between males and females in the quality of diet resulting from ecological competition and segregation between the sexes, as suggested in previous work (Clutton-Brock et al., 1982, 1987; Staines et al., 1982; Illius & Gordon, 1987; Mysterud, 2000; Conradt et al., 2001; Bonenfant et al., 2003; Loe et al., 2003), and (2) selection pressure to compensate for reduced tooth efficiency and to maintain performance during the relatively short reproductive lifespan of males, as shown in the present study. In support of this second view, Hunt et al. (2004) found contrasting results for female and male field crickets reared with extra high-protein diets. Both sexes may invest extra resources either in maintenance for longer reproductive lifespan or in maximizing current reproduction at the expense of longevity. The results indicated that females lived longer but males increased their investment in sexual advertisement and died earlier (Hunt et al., 2004).

Provided that differences found in the present study between males and females are ultimately caused by the operation of sexual selection in polygynous systems (Ralls et al., 1980; Promislow, 1992; Owen-Smith, 1993; Pérez-Barbería, Gordon & Pagel, 2002; Isaac, 2005), we would expect similar patterns in other species. Thus, the generality of the assumed relationship between tooth wear and poor condition of individuals and populations should be revised. Our results suggest that, at least for large polygynous herbivores, females may tend to follow these relationships during some period of their lives, but not so males. Most importantly, the relationship between the degree of previous tooth wear and current performance is not purely mechanistic, but should be mediated by the strategy of compensation employed by each sex as a solution of the trade-off between current performance and bodily maintenance. Future work may address the behavioural tactics involved in dentine depletion patterns in males and females, such as rumination time and particle comminution, as well as their generalization to other polygynous herbivores.

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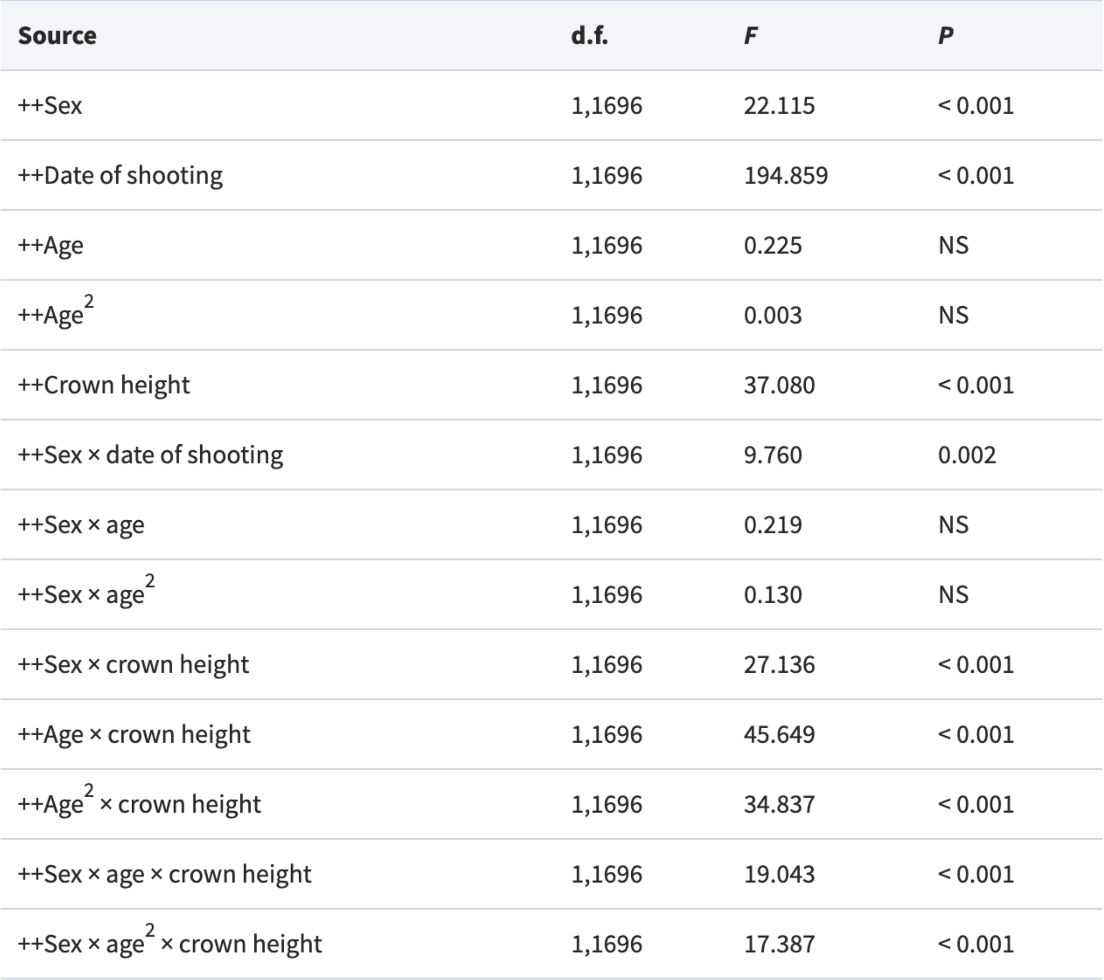
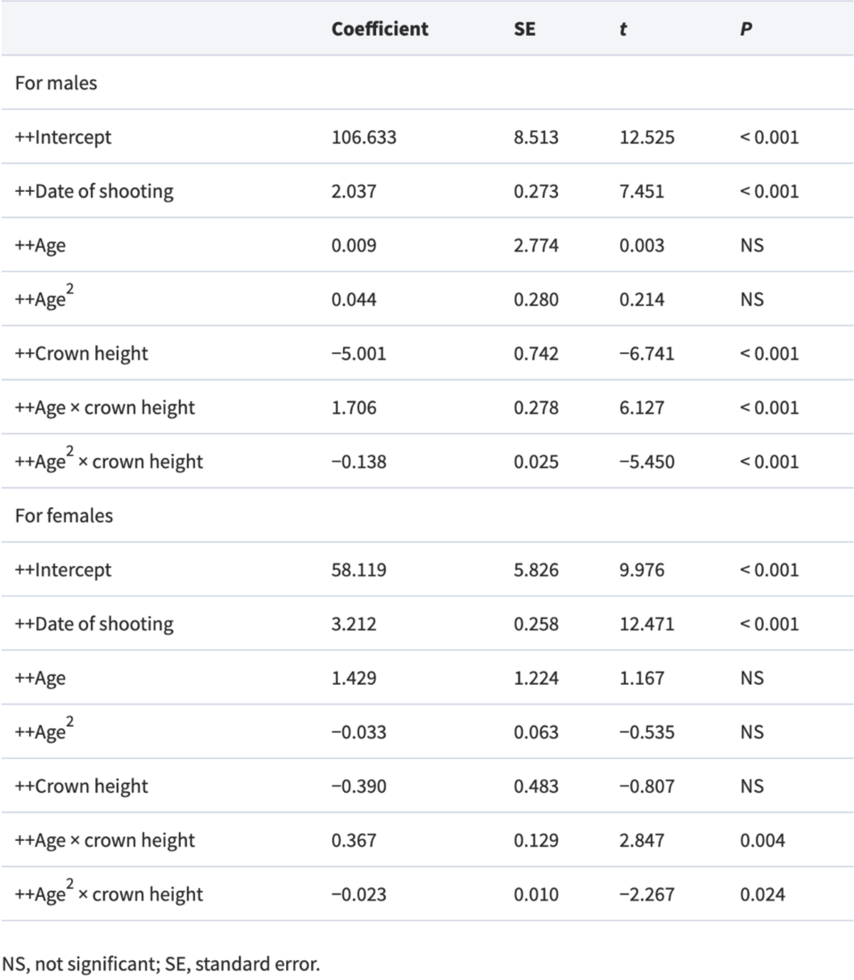
Table 1. Effect of mandibular first molar (M1) crown height on body mass as a measure of performance in females and males



Source	**d.f.**	***F***	***P***
++Sex	1,1696	22.115	< 0.001
++Date of shooting	1,1696	194.859	< 0.001
++Age	1,1696	0.225	NS
++Age^2	1,1696	0.003	NS
++Crown height	1,1696	37.080	< 0.001
++Sex × date of shooting	1,1696	9.760	0.002
++Sex × age	1,1696	0.219	NS
++Sex × age^2	1,1696	0.130	NS
++Sex × crown height	1,1696	27.136	< 0.001
++Age × crown height	1,1696	45.649	< 0.001
++Age^2 × crown height	1,1696	34.837	< 0.001
++Sex × age × crown height	1,1696	19.043	< 0.001
++Sex × age^2 × crown height	1,1696	17.387	< 0.001

The results of the GLM are presented with body mass as dependent variable, and sex and crown height as independent ones. Other covariates (age and date of shooting) were included in the model as control variables. The quadratic value of age was also added to account for the type of relationship between age and body mass. All interactions between the factor (sex) and covariates were significant, thus parameter estimates were calculated separately for males and females, see Table 2.
Adjusted R2 = 0.627.
d.f., degrees of freedom; NS, not significant.

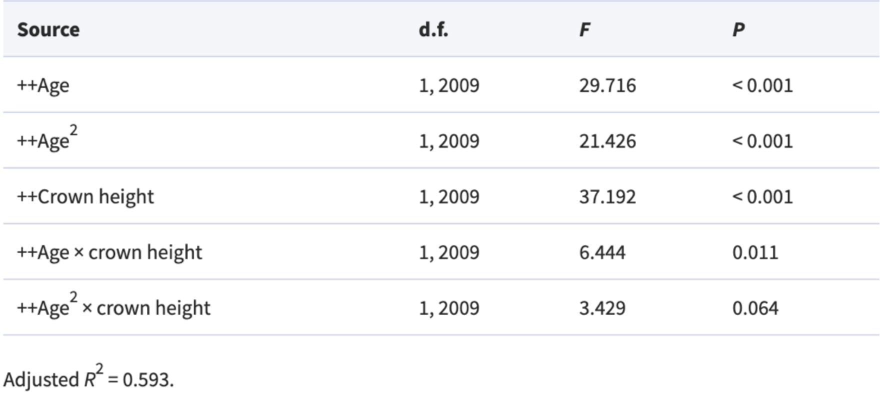
Table 2. Parameter estimates for males and females for the GLM of Table 1 with body mass as the dependent variable



	Coefficient	**SE**	***t***	***P***
For males				
++Intercept	106.633	8.513	12.525	< 0.001
++Date of shooting	2.037	0.273	7.451	< 0.001
++Age	0.009	2.774	0.003	NS
++Age^2	0.044	0.280	0.214	NS
++Crown height	−5.001	0.742	−6.741	< 0.001
++Age × crown height	1.706	0.278	6.127	< 0.001
++Age^2 × crown height	−0.138	0.025	−5.450	< 0.001
For females				
++Intercept	58.119	5.826	9.976	< 0.001
++Date of shooting	3.212	0.258	12.471	< 0.001
++Age	1.429	1.224	1.167	NS
++Age^2	−0.033	0.063	−0.535	NS
++Crown height	−0.390	0.483	−0.807	NS
++Age × crown height	0.367	0.129	2.847	0.004
++Age^2 × crown height	−0.023	0.010	−2.267	0.024

NS, not significant; SE, standard error.

Table 3. Effect of first molar (M1) crown height on antler size



Source	**d.f.**	***F***	***P***
++Age	1, 2009	29.716	< 0.001
++Age^2	1, 2009	21.426	< 0.001
++Crown height	1, 2009	37.192	< 0.001
++Age × crown height	1, 2009	6.444	0.011
++Age^2 × crown height	1, 2009	3.429	0.064

Adjusted R^2 = 0.593.

Table presents the results of the GLM with antler size (principal components analysis scores) as dependent variable, crown height as the independent one and centred-age and its quadratic value as control variables.
d.f., degrees of freedom.

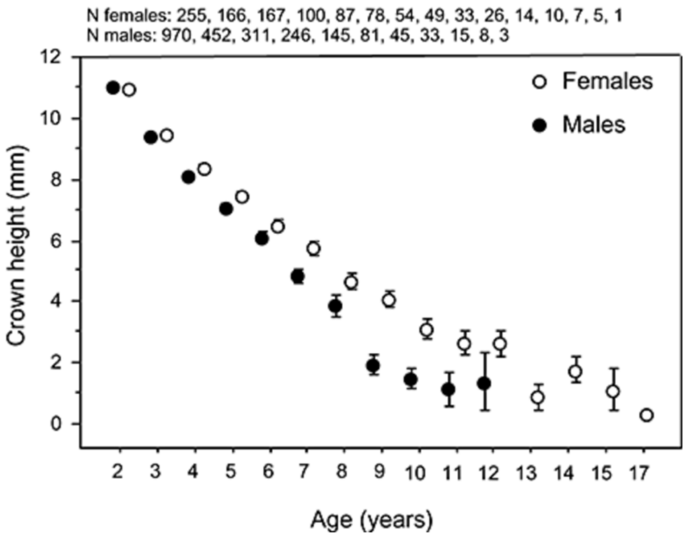


Figure 1. Variation of crown height (mean ± standard error) of mandibular first molar (M1) throughout age (years) for males and females. N, sample size for each age class.

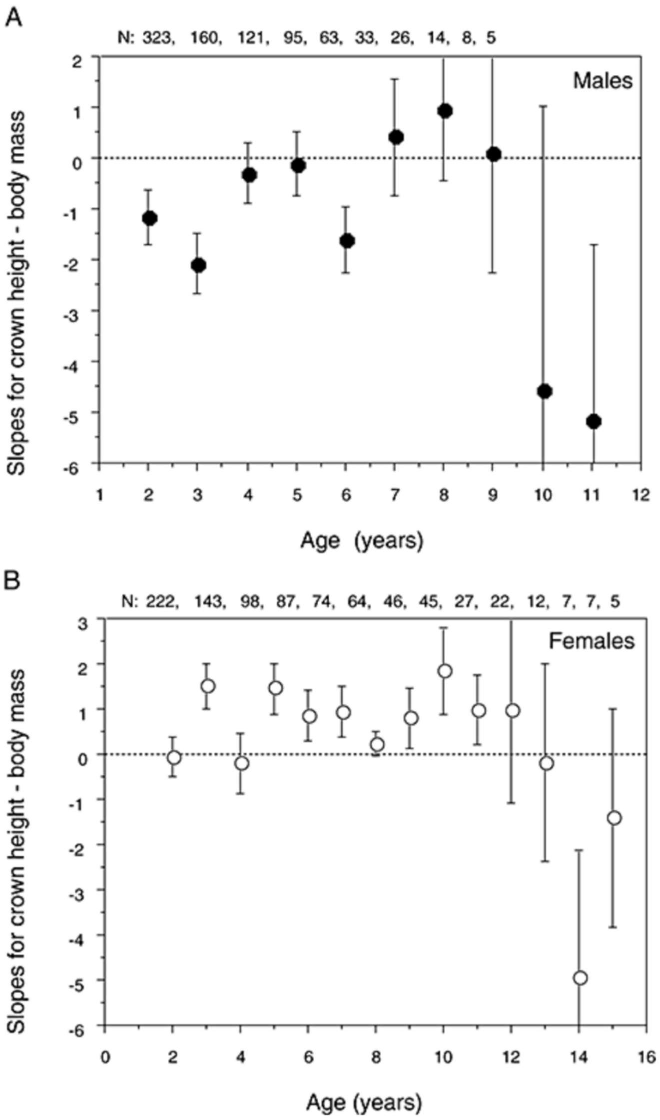


Figure 2. Relationship between tooth wear and body mass throughout life for males (A) and females (B). The slopes (± standard error) of the linear relationships between 'adjusted body mass' and 'adjusted crown height' are shown for each age with a quadratic regression line fitted to these slopes. Positive slopes predominate for females, meaning lower body mass when there are more worn teeth, and negative slopes predominate for males, meaning higher body mass when there are more worn teeth. 'Adjusted body mass' and 'adjusted crown height' are the residuals after controlling for age, age squared, and date of shooting. N, sample size for each age class.

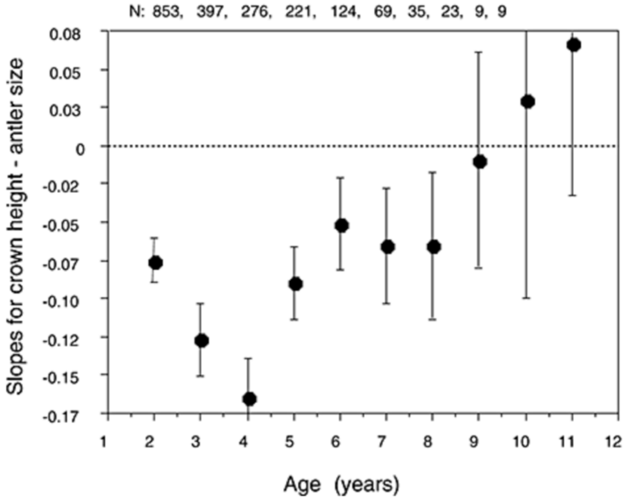
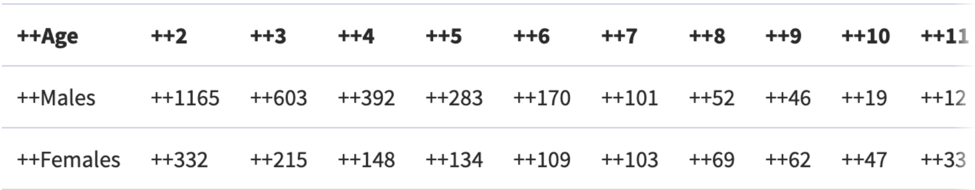


Figure 3. Relationship between tooth wear and antler size across males lifespan. Graph shows the slopes (± standard error) of the linear regressions between crown height of mandibular first molar (M1) and antler size (principal components analysis scores) for each age with a quadratic regression line fitted to these slopes. Slopes were negative, meaning larger antlers when there are more worn teeth, until the end of reproductive age. Antler size scores and crown height were adjusted by removing the effect of age and age squared. N, sample size for each age class.

Appendix

Total sample size for all ages in males and females



++Age	**++2**	**++3**	**++4**	**++5**	**++6**	**++7**	**++8**	**++9**	**++10**	**++11**
++Males	++1165	++603	++392	++283	++170	++101	++52	++46	++19	++12
++Females	++332	++215	++148	++134	++109	++103	++69	++62	++47	++33