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Decelerating and sex-dependent tooth wear in Norwegian red deer

Received: 21 August 2002 / Accepted: 20 January 2003 / Published online: 14 February 2003
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Abstract In ungulates, tooth wear is often suggested as a proximate cause of senescence. Tooth wear is expected to be sex-dependent since energetic requirements and food selection varies largely between sexes in sexually dimorphic ungulates. Furthermore, tooth wear may lower mastication efficiency, and we predict a negative correlation between tooth wear and body weight or condition. We tested these predictions on data on tooth wear (estimated as height of first molar) of 1,311 male and 1,348 female red deer (*Cervus elaphus*) aged 3–25 years and harvested along the west coast of Norway. The rate of tooth wear decreased with age. Males wear teeth at a higher rate (from 0.61 mm/year in 4-year olds to 0.45 mm/year in 11-year olds) than females (from 0.52 mm/year in 4-year olds to 0.39 mm/year in 11-year olds). Molar height correlated positively with body weight in both sexes, but not after adjusting for body size. Molar height was strongly dependent on body size in 3-year-old individuals (when tooth wear is minimal). Earlier reports in the literature of a positive correlation between tooth height and body weight may therefore be due to initial size differences rather than differences in condition due to tooth wear.

Keywords Ageing · Demography · Life history · Mastication · Senescence

Introduction

Rates of survival and reproduction in iteroparous ungulates typically peak for prime-aged individuals (Caughley

1966; Gaillard et al. 1998, 2000a). The progressive loss of function accompanied by decreased performance with increasing age, termed senescence, has lately received much attention. Survival (Gaillard et al. 1998, 2000a; Loison et al. 1999), reproduction (Bérubé et al. 1999; Ericsson et al. 2001; Weladji et al. 2002; Mysterud et al. 2002b; McElligott et al. 2002) and body weight (Mysterud et al. 2001c; Yoccoz et al. 2002) are all traits of performance reported to decrease with age. While the main patterns of senescence are well known in ungulates, much less is known regarding the proximate causes. In general, the disposable soma hypothesis, explaining senescence in terms of a trade-off between soma repair and reproduction or thermogenesis, has received most support as the mechanistic basis for senescence in animals (see Kirkwood and Austad 2000 for a review). This hypothesis is closely related to the (antagonistic) pleiotropy hypothesis suggesting that genes with good early effects would be favoured by selection even if these genes had bad effects at later ages (Williams 1957). In ungulates, however, tooth wear is the most commonly suggested proximate cause of senescence (Tyler 1987; Gaillard et al. 1993; Ericsson and Wallin 2001).

Ruminants are totally dependent on symbiotic microorganisms to break down plant cell walls. Fermentation rates are strongly affected by the size of the food particles presented to the microflora. Because symbiotic microorganisms in the rumen are inefficient in reducing particle size, the physical degradation of forage through chewing is vital to increase its surface area, and thereby increase fermentation rate and reduce the lag to cell wall degradation (McArthur and Sanson 1988; Pérez-Barbería and Gordon 1998a). The process of mastication may therefore be as important for energy uptake as quality of ingested food per se (Dean et al. 1980). Worn teeth, in turn, reduced markedly the ability to masticate (Severinghaus 1949), and increased tooth wear correlated with lower body weight in wild and semi-domestic reindeer (*Rangifer tarandus*; Skogland 1988; Kojola et al. 1998). Despite this, studies relating variation in the pattern of how teeth wear to the pattern of senescence are lacking.

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Body-size is a major factor in the nutritional ecology of large herbivores (Demment and Van Soest 1985). The Jarman-Bell principle states that since the relative energy requirements decrease with increasing body-size ($\text{weight}^{0.75}$), while rumen volume is isometric with size, large herbivores can survive on a lower quality diet than smaller ones (Bell 1971; Jarman 1974; Geist 1974). In sexually dimorphic ungulates, the sexes therefore often differ in food choice (Clutton-Brock et al. 1982; Myrsterud 2000). Since tooth wear may depend on type of food, sex-dependent tooth wear can be expected. As males are larger, they often eat a lower quality diet, and we predict that males wear teeth at a higher rate than females (see also Van Deelen et al. 2000; Ericsson and Wallin 2001).

In this study, we report tooth wear patterns based on 1,311 male and 1,348 female red deer (*Cervus elaphus*; 3 years and older; females up to 25 years of age; males up to 18 years of age) harvested along the west coast of Norway. We analyse the pattern of wear (i.e. stable, decreasing or increasing wear rate with increasing age) and test whether males have a faster tooth wear than females. Finally, we test whether there is a negative correlation between tooth wear and body weight and condition.

Materials and methods

Study area

The study area is the western part of southern Norway, which is the main area for red deer in Norway (Langvatn et al. 1996; Myrsterud et al. 2000, 2001c). Data come from 42 municipalities in the counties of Rogaland (3), Hordaland (15), Sogn og Fjordane (12), Møre og Romsdal (2), Sør-Trøndelag (9), and Nord-Trøndelag (1). Going from south to north, Rogaland and Hordaland are referred to as population P1, Sogn og Fjordane as population P2, Møre og Romsdal and Sør-Trøndelag as population P3, Nord-Trøndelag as population P4, and the island Hitra as population P5 (Myrsterud et al. 2002a). In general, temperature and precipitation decline from south to north and from coast to inland, while snow depth increases along these gradients (Langvatn et al. 1996; Myrsterud et al. 2000). In summer both the length of the growing season and total degree days decline from south-west to north-east (Langvatn and Albon 1986). Topography is generally steeper in inland (Myrsterud et al. 2001a). Hence, the duration of snow cover and timing of plant phenology may vary largely within the study area.

Red deer data

Red deer mandibles were sampled during the annual autumn harvest (between 10 September and 15 November) together with data on body weights and records of date of culling and locality (municipality; see Langvatn et al. 1996; Myrsterud et al. 2002a). The data on tooth wear includes samples from years 1971–1975,

1978, 1981, 1983, 1986 and 2001 (Table 1), and is a subset (determined by access to mandibles) of the data used in earlier analyses of body weight (e.g. Myrsterud et al. 2002a). Hunting is controlled through licenses issued by local wildlife boards in each municipality. Body weight is dressed weight (58% of live weight), i.e. live weight minus head, skin, viscera, bleedable blood and metapodials (Langvatn 1977). Jaw length was measured according to Langvatn (1977). Age was estimated from eruption patterns in younger animals and tooth sectioning (cementum annuli counts) in older deer (Reimers and Nordby 1968; Hamlin et al. 2000).

Estimating tooth wear

Tooth wear was estimated using height of first molar (M_1), which is the most commonly used index of wear (Skogland 1988; Fandos et al. 1993; Ericsson and Wallin 2001; Kojola et al. 1998). Height of M_1 was measured with a digital calliper as the perpendicular (relative to the jawbone) distance from the peak of the distobuccal cusp to the enamel/cementum line (i.e. the stained part of the crown, which corresponds to the so-called clinical crown height in humans).

Statistical analyses

To test for possible nonlinear relationship between molar height (ln-transformed) and age, we used additive models (AM; Venables and Ripley 1999; Hastie and Tibshirani 1990). The complexity of the curve, i.e. the number of degrees of freedom associated with a smoothing spline (df_{spline}), was determined by repeated fitting of the AM. We fitted the model with varying df_{spline} for one variable and held df_{spline} for the other variables constant. Thereafter we tested the fit of the different models in an ANOVA setting (Venables and Ripley 1999). Separate AM were used for males and females.

Linear models (LM; McCullagh and Nelder 1989) are preferred when testing for interactions. To test for sexual differences in tooth wear (i.e. an interaction between sex and age), we first identified the age span in which tooth wear increased linearly with age in both females and males using AM. We then used LM on this subset of age classes.

We also used LM when analysing the possible effect of tooth wear on body weights, as we already know which factors are nonlinear due to previous analyses of body weight in Norwegian red deer (e.g. Myrsterud et al. 2001c, 2002a; Yoccoz et al. 2002). Body weight of red deer follows the three-stage Caughley-like pattern typical of mammals (Caughley 1966; Gaillard et al. 1998, 2000a; Myrsterud et al. 2001c). We therefore used a three-stage model for age with thresholds at 4.5 and 6.5 years of age for females, and 5.5 and 8.5 years of age for males (cf. Myrsterud et al. 2001a). Thresholds were estimated by minimising the Residual Sum of Squares (Myrsterud et al. 2001a). As these thresholds were different in males and females (Myrsterud et al. 2001a, 2001c), separate LMs were used for each sex. Factors influencing body weight of this population of red deer had been extensively analysed earlier (e.g. Myrsterud et al. 2002a), and tooth height was entered together with the covariates density (Myrsterud et al. 2001c), cohort density (Myrsterud et al. 2002a), the North Atlantic Oscillation (NAO) winter index for the previous winter and when in utero (Post et al. 1997; Myrsterud et al. 2001b), distance from the coast, degree of latitude (Langvatn and Albon 1986), diversity of altitudes, diversity of aspects and proportion of high altitude habitat

Table 1 Number of red deer harvested along the west coast of Norway from 1971 to 2001 included in the study

Age (years)	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	25
Females	385	184	160	134	105	80	71	45	36	37	29	20	19	11	9	5	8	3	4	2	1
Males	620	261	160	95	59	37	24	16	16	7	5	6	3	1		1					

(Mysterud et al. 2001a), and the categorical variable “Population” (Mysterud et al. 2000, 2001b, 2001c). As the effect of the NAO (Mysterud et al. 2001b) is expected to be nonlinear, we also considered higher order polynomials. Models were run both with and without including jawbone length in the model. The residual between body weight and jawbone length (an index for body size) is often assumed to reflect body condition (Green 2001).

To facilitate the interpretation of interactions between continuous predictor variables, we considered a multiplicative term of the standardised (mean 0, variance 1) variables (Portier et al. 1998; Mysterud et al. 2000). When variables are standardised, the coefficient for a variable is the strength of this variable when the other variables are at their average values (because the interaction term is then 0). All statistical analyses were performed in the statistical package S-Plus (Venables and Ripley 1999).

Results

Pattern of tooth wear

The height of M_1 peaked at 3 years of age in both sexes [$\ln(M_1 \text{ height } 3 \text{ year}) - \ln(M_1 \text{ height } 2 \text{ year})$; female: mean 0.0319, SE =0.0086, $t = 3.728$, $p < 0.001$; male: mean 0.0215, SE =0.0068, $t = 3.139$, $p = 0.002$]. After this age, tooth wear with age was still nonlinear, but monotonic (AM; females: $df_{\text{spline}} 4$ versus 5, $F = 7.42$, $p = 0.007$; $df_{\text{spline}} 3$ versus 4, $F = 5.97$, $p = 0.015$). The shape of the curve for molar height-age was concave (Fig. 1).

To be able to test properly for sex-dependence in tooth wear (i.e. an age*sex interaction in a LM setting), we restricted the analysis to the part where the relationship between wear and age was linear on a log-scale. This was between 4 and 11 years of age in both sexes (AM; $df_{\text{spline}} 2$ versus 1, $p > 0.05$ in both sexes; i.e. a linear relationship). As predicted, males wore teeth at a higher rate than females (Table 2). The log-linear relationship between tooth wear and age indicates that on a normal scale annual wear gradually declines with age also within this age interval. Annual wear in females declined from 0.52 mm at 4 years of age to 0.39 mm at 11 years of age, while the corresponding values in males are 0.61 and 0.45 mm/year at 4 and 11 years of age, respectively (Fig. 2).

The relationship between molar height and body size

The relationship between tooth size and body size is not trivial since permanent teeth are fully developed at onset of adulthood in ungulates (e.g. Brown and Chapman 1991), while skeletal growth may continue into adult-

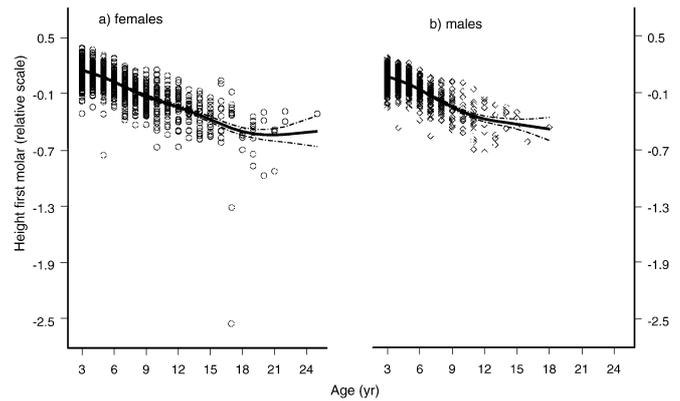


Fig. 1 The non-linear and concave relationship between tooth wear and age in female (a) and male (b) red deer fitted with additive models (females: $df_{\text{spline}}=5$; males: $df_{\text{spline}}=4$). Note that values on the y-axis (relative tooth height) are not comparable for males and females

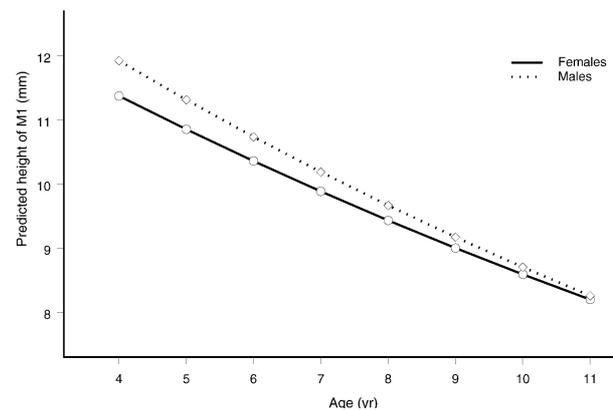


Fig. 2 Predicted values of height of first molar (M_1 ; in mm) in 4- to 11-year-old male and female red deer (males: $M_1 \text{ pred} = e^{2.6887-0.0525 \cdot \text{age}}$; females: $M_1 \text{ pred} = e^{2.6187-0.0468 \cdot \text{age}}$). Note that molars are initially higher in males since they have a larger body size

hood. Considering only 3-year olds, in which we can assume that height has reached the fully grown level and wear is minimal, there was a clear positive correlation between molar height (\ln -transformed) and jawbone size (females: mean =0.637, SE =0.183, $t = 3.49$, $p = 0.0005$; males: mean =0.864, SE =0.105, $t = 8.22$, $p < 0.0001$; in males the relationship was only close to linear, but monotonic).

Table 2 The relationship between height of first molar (M_1 ; \ln -transformed) and independent variables. Parameter estimates [obtained from the linear model, i.e. least square (LS) estimates, and from 1,000 parametric bootstrap replicates] with bootstrapped standard errors and confidence intervals (CI)

Parameter	LS estimate	Bootstrap estimate	Bootstrap SE	95% CI
Intercept	-1.88	-1.88	0.488	-2.86, -0.904
Age	-0.0497	-0.0497	0.00179	-0.0533, -0.0461
Sex	0.0256	0.0249	0.0187	-0.0125, 0.0622
Jaw length	0.804	0.805	0.0873	0.631, 0.980
Age * Sex	-0.00799	-0.00790	0.00293	-0.0138, -0.00204

Table 3 The relationship between body weight (dependent variable; ln-transformed) and various independent variables in female and male red deer when excluding and including body size. Parameter estimates [obtained from the general linear model, i.e. least square (*LS*) estimates, and from 1000 parametric bootstrap replicates] with bootstrapped standard errors (*Bootstrap SE*) and confidence intervals (*CI*). Results for molar height are in *bold* (*NAO* North Atlantic oscillation)

Parameter	LS estimate	Bootstrap estimate	Bootstrap SE	95% CI
Females – excluding jaw length				
Intercept	3.32	3.34	0.597	2.14, 4.53
Age 3–4 years	0.0236	0.0238	0.00872	0.00633, 0.0412
Age 5–6 years	0.0267	0.0265	0.00756	0.0114, 0.0416
Age 7–20 years	–0.000107	–0.000190	0.00194	–0.00406, 0.00368
Molar height	0.0204	0.0204	0.00786	0.00468, 0.0361
Age x Molar height	–0.000718	–0.000711	0.000647	–0.00200, 0.000582
Density	0.0270	0.0275	0.0230	–0.0186, 0.0735
Cohort density	–0.0171	–0.0181	0.0254	–0.0688, 0.0327
Date of culling	–0.000561	–0.000564	0.000170	–0.000903, –0.000224
Diversity of altitude habitats	–0.0166	–0.0148	0.0286	–0.0720, 0.0425
Proportion of high altitude habitats	0.113	0.113	0.0294	0.0539, 0.172
Diversity of aspects	0.295	0.286	0.286	–0.286, 0.858
NAO	–0.00194	–0.00178	0.00941	–0.0206, 0.0170
(NAO) ²	–0.00531	–0.00540	0.00367	–0.0127, 0.00194
(NAO) ³	0.00419	0.00415	0.00245	–0.000747, 0.00905
Distance from the coast	0.0101	0.0101	0.0136	–0.0172, 0.0373
Proportion of meadow	1.27	1.27	0.298	0.670, 1.86
Population (P2-P1)	0.0363	0.0360	0.0101	0.0157, 0.0562
Population (P3-P1)	0.100	0.0992	0.0121	0.0751, 0.123
Population (P4-P1)	0.0699	0.0716	0.0285	0.0145, 0.129
Population (P5-P1)	–0.0773	–0.0748	0.0395	–0.154, 0.00424
Males – excluding jaw length				
Intercept	4.53	4.53	1.44	1.65, 7.41
Age 4–5 years	0.0550	0.0549	0.0144	0.0261, 0.0836
Age 6–8 years	–0.00456	–0.00459	0.0122	–0.0289, 0.0197
Age 9–11 years	0.00420	0.00491	0.0186	–0.0322, 0.0421
Age x Date of culling	–0.0147	–0.0149	0.00385	–0.0226, –0.00719
Molar height	0.0731	0.0733	0.0219	0.0295, 0.117
Age x Molar height	–0.00803	–0.00803	0.00338	–0.0148, –0.00127
Density	0.236	0.238	0.100	0.0370, 0.438
Cohort density	–0.199	–0.200	0.0823	–0.365, –0.0355
Date of culling	0.00705	0.00842	0.0221	–0.0358, 0.0526
Age x Density	–0.0146	–0.0145	0.00570	–0.0259, –0.00312
Age x Date of culling x Density	0.000909	0.000875	0.00121	–0.00155, 0.00329
Diversity of altitude habitats	–0.113	–0.114	0.0458	–0.206, –0.0228
Proportion of high altitude habitats	–0.0379	–0.0368	0.0590	–0.155, 0.0813
Diversity of aspects	–0.0687	–0.0638	0.699	–1.46, 1.33
NAO	0.0190	0.0194	0.0172	–0.0149, 0.0537
(NAO) ²	–0.00669	–0.00683	0.00801	–0.0228, 0.00918
(NAO) ³	–0.00160	–0.00158	0.00473	–0.0110, 0.00788
Cohort NAO	0.00205	0.00206	0.00356	–0.00506, 0.00917
Distance from the coast	0.0936	0.0936	0.0263	0.0410, 0.146
Proportion of meadow	0.269	0.264	0.528	–0.793, 1.32
Population (P2-P1)	0.0235	0.0229	0.0217	–0.0206, 0.0663
Population (P3-P1)	0.0958	0.0956	0.0237	0.0481, 0.143
Population (P4-P1)	–0.0219	–0.0238	0.0557	–0.135, 0.0876
Population (P5-P1)	–0.238	–0.242	0.0710	–0.384, –0.100
Females – including jaw length				
Intercept	–7.20	–7.18	0.831	–8.84, –5.52
Jaw length	1.95	1.95	0.123	1.70, 2.19
Age 3–4 years	0.00129	0.00149	0.00796	–0.0144, 0.0174
Age 5–6 years	0.0156	0.0153	0.00634	0.00264, 0.0280
Age 7–20 years	–0.00196	–0.00193	0.00173	–0.00540, 0.00153
Molar height	0.00622	0.00643	0.00687	–0.00731, 0.0202
Age x Molar height	0.0000884	0.0000797	0.000571	–0.00106, 0.00122
Density	0.000533	0.00172	0.0212	–0.0407, 0.0442
Cohort density	0.00322	0.00334	0.0222	–0.0411, 0.0477
Date of culling	–0.000637	–0.000625	0.000153	–0.000931, –0.000319
Diversity of altitude habitats	0.00642	0.00620	0.0257	–0.0452, 0.0576
Proportion of high altitude habitats	0.100	0.102	0.0271	0.0474, 0.156
Diversity of aspects	0.148	0.138	0.246	–0.354, 0.631
NAO	–0.00469	–0.00472	0.00872	–0.0222, 0.0127
(NAO) ²	–0.00650	–0.00650	0.00356	–0.0136, 0.000615

Table 3 (continued)

Parameter	LS estimate	Bootstrap estimate	Bootstrap SE	95% CI
(NAO) ³	0.00409	0.00412	0.00234	-0.000556, 0.00880
Distance from the coast	0.00877	0.00895	0.0123	-0.0156, 0.0335
Proportion of meadow	0.986	0.984	0.264	0.456, 1.51
Population (P2-P1)	0.0365	0.0365	0.00866	0.0192, 0.0538
Population (P3-P1)	0.0782	0.0784	0.0113	0.0559, 0.101
Population (P4-P1)	0.0126	0.0140	0.0270	-0.0400, 0.0679
Population (P5-P1)	-0.0108	-0.0111	0.0361	-0.0834, 0.0611
Males – including jaw length				
Intercept	-13.2	-13.2	1.56	-16.4, -10.1
Jaw length	3.03	3.03	0.178	2.67, 3.38
Age 4–5 years	0.0385	0.0387	0.0111	0.0166, 0.0608
Age 6–8 years	-0.00775	-0.00800	0.00949	-0.0270, 0.0110
Age 9–11 years	-0.0143	-0.0137	0.0150	-0.0438, 0.0164
Age x Date of culling	-0.0120	-0.0120	0.00316	-0.0183, -0.00565
Molar height	0.0167	0.0171	0.0175	-0.0179, 0.0522
Age x Molar height	-0.00317	-0.00326	0.00268	-0.00863, 0.00210
Density	0.0640	0.0658	0.0773	-0.0887, 0.220
Cohort density	-0.0370	-0.0387	0.0654	-0.170, 0.0921
Date of culling	-0.0145	-0.0147	0.0179	-0.0505, 0.0211
Age x Density	-0.00534	-0.00540	0.00427	-0.0139, 0.00314
Age x Date of culling x Density	0.00207	0.00209	0.000982	0.000123, 0.00405
Diversity of altitude habitats	-0.00637	-0.00447	0.0363	-0.0770, 0.0681
Proportion of high altitude habitats	0.0213	0.0213	0.0468	-0.0723, 0.115
Diversity of aspects	0.178	0.194	0.541	-0.889, 1.28
NAO	0.00530	0.00418	0.0138	-0.0235, 0.0319
(NAO) ²	-0.00781	-0.00786	0.00671	-0.0213, 0.00556
(NAO) ³	0.00158	0.00179	0.00396	-0.00613, 0.00971
Cohort NAO	0.00203	0.00191	0.00273	-0.00355, 0.00736
Distance from the coast	0.0342	0.0342	0.0215	-0.00882, 0.0773
Proportion of meadow	0.459	0.439	0.434	-0.429, 1.31
Population (P2-P1)	0.0136	0.0140	0.0184	-0.0228, 0.0508
Population (P3-P1)	0.0561	0.0568	0.0193	0.0182, 0.0953
Population (P4-P1)	-0.107	-0.107	0.046	-0.199, -0.0151
Population (P5-P1)	-0.0549	-0.0524	0.0540	-0.160, 0.0557

The relationship between molar height and body weight

There was a positive correlation between molar height and body weight in both males and females (Table 3). When entering jawbone length as a covariate in the model, and thus arguably measuring condition, the positive correlation between molar height and body weight was no longer significant (Table 3). In the models, we also included several other variables known to affect body weight (Table 3), since fitting a too complex model would result in estimates with lower bias but lower precision, and it is most important to lower bias as much as possible (Cochran and Rubin 1973). As this is a small subset of a previous analysis on body weight, several of these covariates were not significant here, and there was some discrepancy in spatial covariates due to only 42 municipalities being included in this study, while data on body weight were available for 106 municipalities in the total dataset; see Myrsetrud et al. (2001a, 2002a) for a more full account of these results.

Discussion

Tooth wear as a proximate cause of senescence

The patterns of senescence in survival, reproduction and body weight are well documented in ungulates (see Introduction), including the Norwegian red deer populations under study here (Myrsetrud et al. 2001c; Yoccoz et al. 2002). These performance traits are without exception nonlinearly related to age, and the curvature is always convex. Despite tooth wear being frequently suggested to form the mechanistic basis of senescence in ungulates (e.g. Gaillard et al. 1993; Tyler 1986; Ericsson and Wallin 2001), we found that there was progressively less wear with age. This suggests that the role of tooth wear as a component in the process of senescence may be overrated. Furthermore, this observation does not support the suggestion that mastication at a young age is more efficient, thus delaying wear (Lanyon and Sanson 1986). However, our observations are supported by reports in the literature; wear rates of 7- to 10-year-old female caribou were lower than for 3- to 7-year-old females ($n = 337$; Miller 1974), and there was no increase in wear after the age of 8 years in female Svalbard reindeer (*Rangifer tarandus platyrhynchus*; $n = 81$; Tyler 1986). When using

transversal data (as we do), one must realise that the average quality of individuals may increase with age since poor quality individuals die first (Gaillard et al. 2000b). However, as the decelerating tooth wear was also evident for age classes between 3 and 7 years, for which natural mortality is very low (Gaillard et al. 1998, 2000a; see Langvatn and Loison 1999 for Norwegian red deer), it seems unlikely that this can account for the pattern of decelerating wear with age reported here.

As cusps are worn down the topography of the molar flattens, i.e. more material has to be worn for every mm decrease in tooth height. Furthermore, the maximal buccolingual width of the molars is in the cervical area of the tooth crown (Kierdorf and Becher 1997); molars have a slightly conical shape and surface area may increase as teeth are worn. This may provide a mechanistic explanation of the observed decrease in tooth wear (as measured by molar height) with increasing age.

Sex-dependent tooth wear rates

Most attempts to determine age by wear have proven unreliable (Cederlund et al. 1991; Hewison et al. 1999), and the variation in tooth wear between the sexes (Thomas and Bandy 1975; Moore et al. 1995; Van Deelen et al. 2000) has been viewed as a problem for age determination rather than a possibility to gain insight into life history variation (but see Skogland 1988; Hewison et al. 1999; Ericsson and Wallin 2001; Loison et al. 2001 for notable exceptions). Sex differences in tooth wear are predicted from knowledge of food selection in sexually dimorphic species (e.g. Illius and Gordon 1987). Our study, testing explicitly for a sex and age interaction, supported the finding that males wear teeth faster than females. Ericsson and Wallin (2001) also tested for such an interaction, but they included different age classes for males and females and tests of interactions are then unreliable due to imbalance in the data. Despite differences in methodology, all reported patterns, including our study, suggest that males wear teeth faster than females. Although we suggest that the mechanism is food choice, this is not the only possibility. As males have a shorter life expectancy than females in most ungulate species and also grow faster, males may also have faster tooth wear due to grinding food more thoroughly. However, empirical evidence suggests the opposite. In Nubian ibex (*Capra nubiana*), females had a higher chewing rate than males (Gross et al. 1995). This may possibly be to compensate for a smaller body size, which may require a higher nutritional quality (which may be gained by grinding forage more thoroughly if high quality forage is not readily available). So for the moment, sex-dependent food selection seems to be the most plausible explanation of the faster tooth wear in male ungulates.

Relationship between tooth wear and body weight and condition

That tooth wear decreases chewing efficiency in mammals has been demonstrated in several studies. In koala (*Phascolarctos cinerus*), an increase in tooth wear was correlated with an increase in the average amount of time spent feeding, the average number of daily chews, the number of chews per leaf and average chew rate, and in the average number of leaves consumed (Logan and Sanson 2002). Koalas with extensive tooth wear were found to have much larger particles and a greater proportion of these present in the stomach than animals with less worn teeth (Lanyon and Sanson 1986). There was also a correlation between tooth wear and mastication ability in red deer (Pérez-Barbería and Gordon 1998b). In turn, there was a positive relationship between molar height and body weight or condition reported in reindeer (Skogland 1988; Kojola et al. 1998). Molar height in semi-domestic reindeer in Finland depended on the mean standing crop of terrestrial lichens in winter habitats, and the extent of tooth wear had the strongest effect on body weight (Kojola et al. 1998). In turn, mortality was associated with the degree of molar wear in Svalbard reindeer (Tyler 1986). With increasing tooth wear, females had progressively depleted fat reserves. In all of these studies (except Tyler 1986), tooth height was used as a measure of wear and tested directly against body weight. Also for Norwegian red deer, tooth height was positively related to body weight in both sexes. However, this was not evident after adjusting for jaw length (a measure of body size), which warrants some cautionary notes.

The crown formation of M_1 is complete at the age of 4 months (Brown and Chapman 1991), and M_1 is fully erupted at 1 year of age in mule deer (*Odocoileus hemionus*; Robinette et al. 1957; Rees et al. 1966). Wear starts as soon as M_1 is functional (Brown and Chapman 1991; Kierdorf and Becher 1997). However, height of M_1 peaked at 3 years of age in this study on red deer and in a previous study of caribou (Miller 1974). This apparent increase in height may be due to the inclination of the tooth relative to the jaw, as tooth height is measured perpendicular to the jawbone. As maximum height of M_1 was reached at 3 years of age in red deer, we used this age-class and found a positive correlation between jaw size and height of M_1 . Assuming little wear at this stage, large sized 3-year-old deer would start their adult life with high teeth. If so, one may argue that analyses using molar height as an indicator of wear should include a measure of body size as covariate to control for differences in starting point (i.e. initial molar height). Hence, the positive relationship between tooth height and body weight reported for reindeer (Skogland 1988; Kojola et al. 1998) may be confounded by the positive correlation between body size and initial molar height.

Acknowledgements We gratefully acknowledge the financial support of the Research Council of Norway to L.E.L. and A.M. We

thank Nigel G. Yoccoz for statistical advice and Jean-Michel Gaillard, Uwe Kierdorf, Giacomo Tavecchia, and one anonymous referee for comments on an earlier version of the manuscript. Vebjørn Veiberg, Erling Meisingset, Brigte Samdal, Anders B. Martinsen, Tero Klemola, Hege Gundersen and Simen Loe are thanked for assistance during teeth measurements.

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