Does tooth wear influence ageing? A comparative study across large herbivores

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ABSTRACT

We test whether the intensity of tooth wear influences the strength of actuarial senescence across species of large herbivores. We collected from the literature data on tooth wear in the wild (measured as the slope of the regression of log-transformed M1 crown height on age), longevity (measured as the age at which 90% of individuals are dead) and two metrics of actuarial senescence in captive populations (rate of senescence between 6 and 12 years of age and Gompertz rate of senescence). Between-species differences and variation in tooth height accounted for most of the observed variation in tooth wear among large herbivores: tooth height and tooth wear were positively correlated. In contrast, tooth wear was little influenced by sex, body mass, or taxonomy. No marked between-sex differences in longevity occurred. Males senesced faster than females when tooth wear was low (for both senescence metrics), while between-sex differences in actuarial senescence when tooth wear was high depended on the metric used to measure actuarial senescence. While longevity was mostly independent of the intensity of tooth wear, we found general support for a positive relationship between both measures of actuarial senescence and tooth wear. These patterns were consistent whether hypsodonty was controlled for or not. Although varying according to sex and to the metric used for assessing actuarial senescence, our findings suggest overall that tooth wear could be positively associated with actuarial senescence among large herbivores. Further longitudinal studies focusing on changes within individuals will be required to test whether a mechanistic link between tooth wear and actuarial senescence occurs in large herbivores.

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1. Introduction

It is now commonly accepted that most animals age (Nussey et al., 2013), though striking exceptions are regularly documented (Austad, 2010; Jones et al., 2014). Recent studies have revealed that both survival and reproductive success decrease with increasing age in vertebrates (Nussey et al., 2013; Jones et al., 2014), processes that have been called actuarial and reproductive senescence respectively. Senescence patterns vary strongly among species (e.g. Jones et al., 2014) and current studies aim at understanding the factors shaping this variation. For instance, the rate of actuarial senescence correlates with the pace of life in mammals (Jones et al., 2008) and is impacted by environmental conditions (Lemaître et al., 2013). Physiological performance also declines with age in vertebrates (Nussey et al., 2013), as it is the case for body mass (Nussey et al., 2011) and tooth height (Veiberg et al., 2007a; b). However, whether the decline in survival rates is a direct consequence of senescence in physiological traits or functions remains an open question (Promislow et al., 2006). Nevertheless, any reduction in the ability to ingest food could change the actuarial senescence pattern observed at the population level.

Tooth wear is a near universal process among mammals. It is observed in both wild and captive populations (Kaiser et al., 2009) and has long been used to estimate the age of free-living individuals (Severinghaus, 1949). As food processing by mammals strongly depends on the efficiency of teeth (Dean et al., 1980; Fortelius, 1985), increased tooth wear with age should limit resource acquisition and thereby be associated with decreasing performance of individuals. In support of this prediction, a positive link between tooth wear and increased mortality has been repeatedly reported among individuals within a given population (e.g. Klein and Olson, 1960 for mule deer *Odocoileus hemionus*; Stirling, 1969 for Weddell seal *Leptonychotes weddelli*; Lanyon and Sanson, 1986 for koala, *Phascolarctos cinereus*; Skogland, 1988 for reindeer, *Rangifer tarandus*; Owen-Smith, 1993 for greater kudu, *Tragelaphus strepsiceros*; Gaillard et al., 1993 for roe deer *Capreolus capreolus*) or among populations within a given species (Garrott et al., 2003 for elk *Cervus elaphus canadensis*; Veiberg et al., 2007a for roe deer). For example, Garrott et al. (2003) provided clear evidence that elk in the west central part of Yellowstone National Park, where intense geothermal activity accelerates tooth wear through very high fluoride and silica levels, have a much shorter maximal

lifespan (15 years) than elk in the northeast part of the Park (25 years). Moreover, the onset of actuarial senescence occurred six years earlier in the west central part of the Park than in the northeast part (10 vs. 16 years of age, Garrott et al., 2003). On the other hand, the only study to our knowledge that tested for the impact of tooth wear on individual reproductive performance in the wild did not detect any negative influence (Nussey et al., 2007 on red deer, *Cervus elaphus*), although in reindeer, between-population differences in tooth wear of adult females were associated with differences in survival of their offspring (Skogland, 1988). Overall, tooth wear seems to be detrimental for survival at least, and thereby for individual fitness. Thus, animals should have evolved a variety of morpho-physiological adaptations to counter negative effects of tooth wear on fitness. Among these, hypsodonty (i.e. high-crowned teeth) stands out as the most obvious adaptation to prolong functionality, and hence life (Damuth and Janis, 2011).

Two extreme scenarios regarding how actuarial senescence has evolved in response to the tooth wear experienced by individuals of a given species over evolutionary time can thus be expected: (1) average tooth wear provides a clue to the rate of general physiological deterioration of individuals. Under this scenario, we expect actuarial senescence to increase with increasing tooth wear independently of any effect of hypsodonty, which would have evolved only in response to feeding tactics and habitat selection (Mendoza and Palmqvist, 2008); (2) average tooth wear might simply measure the selective pressure for increased hypsodonty, meaning that a proportional relationship between tooth wear and hypsodonty should occur. Under this scenario, actuarial senescence is expected to be independent of the rate of tooth wear for a given hypsodonty. These predictions have not been tested so far. We aim here to fill this gap by assessing the potential link between tooth wear, hypsodonty (measured by tooth height) and metrics of actuarial senescence, using large herbivore species because of the large amount of information on teeth available for this mammalian group.

As a first step, we identify the sources of variation in the intensity of tooth wear by quantifying how tooth height correlates with the rate of tooth wear between sexes and among species of large herbivores. We expect (1) species to have variable intensity of tooth wear due to variable life histories and environmental conditions (e.g. Jurado et al., 2008), (2) species experiencing higher tooth wear to be more hypsodont as young adults (i.e. to start with higher unworn teeth, Damuth and Janis, 2014), and (3) males to show higher intensity of tooth wear than females since large herbivores are mostly polygynous and a substantial amount of energy that males allocate to sexual competition cannot be used for somatic maintenance (Carranza et al., 2004; Lemaître et al., 2015). In a second step, we test whether the intensity of tooth wear predicts the strength of actuarial senescence after accounting for possible confounding effects of species, sex, diet, tooth height, body mass and taxonomic position. We thus ask whether actuarial senescence varies with tooth wear for a given tooth height, and whether actuarial senescence varies with tooth height.

2. Materials and methods

2.1. Dataset

We conducted a literature survey using *Web of Science* (SCI-Expanded) and the keywords 'tooth wear' and 'age' and completed our research by checking papers quoted in two major reviews of this field (Fortelius and Solounias, 2000; Damuth and Janis, 2014). Since most of these studies were focused on crown height of the first mandibular molar (generally named M1), we only considered this tooth in the following analyses. In addition, we found one study on the extinct *Myotragus balearicus* (Jordana et al., 2012) that we did not retain for the analyses because no accurate data on either percentage of grass in the diet nor actuarial senescence were reported. Importantly, to avoid spurious estimates of tooth wear, we have kept only studies where age was estimated independently from tooth height (i.e. either from known-aged individuals

or from the number of cementum lines after tooth sectioning). We thus discarded a few well-known studies of tooth wear (e.g. Mertens, 1984; Spinage, 1972) because in these studies age was estimated from wear. We also restricted the search to studies performed on free-ranging populations, since tooth wear differs markedly between captive and wild animals within a given species of large herbivore (Kaiser et al., 2009; Taylor et al., 2014, 2015). As we aimed to analyse evolutionary links between tooth wear and actuarial senescence, data on tooth wear from free-ranging individuals were better suited for our purpose. Age-specific data on M1 wear were provided by 28 studies on 21 species of wild ungulates (9 Cervidae, 8 Bovidae and 4 others including the pronghorn, *Antilocapra americana* (Antilocapridae) and the giraffe, *Giraffa camelopardalis* (Giraffidae) for the Artiodactyla and the white rhinoceros, *Ceratotherium simum* (Rhinocerotidae) and the zebra, *Equus burchelli* (Equidae) for the Perissodactyla (see Table S1 in data supplement)). It is noteworthy that none of the case studies on tooth wear we identified reported longitudinal data obtained by monitoring the same animals as their age increased. Such cross-sectional data are thus perhaps biased by viability selection (sensu Fisher, 1930), which could lead to under-estimates of the real tooth wear because if animals with smaller teeth were at a selective disadvantage, the average decrease of tooth height with increasing age would be underestimated (a classical side effect of individual heterogeneity, Nussey et al., 2008). For these 21 species, we extracted sex-specific adult body mass (i.e. age after which body growth has stopped) from the literature. In the majority of cases, adult body mass data for males and females came from the same population. When information on tooth wear was not sex-specific, we used an average body mass between sexes.

In order to analyse the relationship between tooth wear and actuarial senescence, we used data on survival for ungulate species living in captivity. In doing so, we do not assume that the measured actuarial senescence in a given population of large herbivore is a direct consequence of the tooth wear and hypsodonty measured in the same population, but rather that the actuarial senescence is a species-specific life-history trait that covaries with other traits to shape the overall life history strategy (as shown by Jones et al., 2008 across mammals and birds and by Garratt et al., 2013 across mammals). Senescence data from captive animals are not affected by confounding effects of many environmentally-driven mortality causes, and thus provide a reliable proxy for the senescence pattern that has evolved for a given species (see Ricklefs, 2010; Tidière et al., 2014 for similar approaches). These senescence data however can be affected by species-specific differences in the success of husbandry. For ruminants, where browsing species are more difficult to keep in captivity, the natural diet (i.e., whether a species is a browser or a grazer) influences the husbandry success (Müller et al., 2010) and hence also senescence measurements (Lemaître et al., 2013). Therefore, to achieve reliable estimates of the strength of actuarial senescence from zoo data, we needed to correct for confounding effects of the natural diet, using the percentage of grass in species' natural diet (hereafter called 'diet') that opposed browsers (typically less than 10% of grass) from grazers (typically more than 90% of grass) (Müller et al., 2011). These data were principally gathered from Zerbe et al. (2012) and supplemented with more specific sources when required (Codron et al., 2007). We obtained survival data from the database International Species Information System (ISIS, see also Müller et al., 2011; Lemaître et al., 2013; Tidière et al., 2014 for more information), which contains data since 1973, from 850 member institutions (zoos, national parks) in over 80 countries. Information such as sex, dates of birth, and date of death is available for each individual. Assuming that the total number of individuals living in zoos for a given species corresponds to a worldwide metapopulation, we computed population parameters for species living in captivity. We only used cohorts of animals for which both dates of birth and death were known, which implies that all animals were born in captivity. Although differences in veterinary care might differ between zoos, several

different species are kept at any one institution, and all species are kept at more than one institution, which buffers the effect of health care provided on animals in the inter-specific analyses.

We considered three distinct metrics to measure survival patterns and the intensity of actuarial senescence. Longevity is the most commonly used measure of survival differences across species (Moorad et al., 2012), so we first used the age at which 90% of individuals have died (hereafter called 'longevity') to avoid problems associated with the use of maximum longevity (see e.g. Moorad et al., 2012). However, longevity does not measure actuarial senescence, so we computed two metrics of actuarial senescence that have been shown to be reliable for describing senescence in survival of large herbivores (see e.g. Lemaître and Gaillard, 2013; Lemaître et al., 2013; Tidière et al., 2014). We used two different metrics of actuarial senescence because they are based on different assumptions and capture different aspects of mortality patterns at old ages. We first measured the rate of senescence between 6 and 12 years of age. These age-thresholds were chosen based on previous detailed analyses of age-specific variation in intensively monitored populations of large herbivores (e.g. Loison et al., 1999; Festa-Bianchet et al., 2003; Gaillard et al., 2004; Toïgo et al., 2007). This rate of senescence measured the proportional decrease in survival between 6 and 12 years of age (see Tidière et al., 2014 for uses of this metric in similar contexts). Then we considered the senescence rate obtained from the Gompertz model (hereafter called 'Gompertz rate'). The Gompertz model is based on the assumption that mortality increases with age during adulthood at a constant exponential rate from a given age (called the onset of senescence, which varies across species). The Gompertz rate provides a reliable description of age-specific survival in large herbivores (Gaillard et al., 2004). In applying the Gompertz model, we first built the capture-recapture history (i.e. which individuals are present at defined points of 'recapture') of each species of large herbivores included in our dataset. These capture histories were then loaded into a CMR (capture-mark-recapture) software (M-SURGE, Choquet et al., 2004) to get reliable age-specific estimates (Lebreton et al., 1992), knowing that detection probabilities were equal to 1 in captivity (as opposed to capture-recapture datasets for wild animals where not all living animals are recaptured at each capture event, Gimenez et al., 2008). We then fit the Gompertz model for the age-range over which tooth wear was measured. Mortality data from the ISIS database were available from life tables built from birth to the oldest age recorded, whereas tooth wear was assessed after the teeth were fully grown. This is an important methodological point, so when the data for estimating the Gompertz rate did not cover the same ages as the tooth wear data, the dataset was discarded, which restricted this specific analysis to 37 populations representing 13 species.

2.2. Analyses

2.2.1. Quantifying the intensity of tooth wear and tooth height

We extracted raw data on age-specific tooth height, using data displayed in tables or in graphs. For the graphs, we extracted data using OOodigitizer version 0.3.1. (http://extensions.services.openoffice.org/) allowing extraction of coordinates from graphs. For all studies, tooth wear was estimated from the relationship between M1 crown height and age over all ages that tooth wear was measured (see Table S1), by fitting either a linear regression of tooth height on age, a quadratic regression of tooth height on age, and lastly a linear regression of log-transformed tooth height on age. All these models outperformed the constant model (i.e. the model with no directional change of tooth height with age). The results are reported in Table S2. From this table it appears that the regression of log-transformed tooth height on age provided a good fit (based on R^2 values) compared to both the linear or quadratic regressions fit to raw data. Although the log-transformation of tooth height led to better fits than the linear or quadratic models in only 14 out of 51 case studies, we selected the log-transformation because an exponential decrease has been used in most recent studies (e.g. Veiberg et al.,

2007b; Ozaki et al., 2010) and obvious deviations from a linear decrease have been reported in some cases (e.g. Loe et al., 2003; Carranza et al., 2008). Based on that evidence, we used the slope of the regression on a log-scale to measure the intensity of tooth wear with increasing age, which prevented us from getting a measure of wear with an interpretable unit, like mm/year. The slope is therefore an index with no unit. This tooth wear index ranged from 0.000633 in one population of female sika deer, *Cervus nippon* (Ozaki et al., 2010) to 0.282 in the combined sexes of elk, *Cervus canadensis* (Klein et al., 1981). Median and mean tooth wear indices were 0.0522 and 0.068, respectively. All subsequent analyses were performed using this metric of tooth wear. We calculated tooth height using the population-specific linear regressions of tooth height (on a log-scale) on age. Specifically, we solved the regression equation between log-tooth height and age at the age at which actuarial senescence began based on the best Gompertz model. For instance, when tooth wear was studied between 2 and 14 years of age in a population in which the onset of actuarial senescence was estimated to be 4 years, we used the equation of the linear regression to calculate tooth height at age 4. Thus, our measure of tooth height originates from the same data as the measures of tooth wear.

2.2.2. Factors associated with tooth wear

We identified associations of body mass, sex, tooth height, taxonomy and species with tooth wear using linear mixed models. Body mass and tooth height were included as continuous covariates, sex as a three level fixed factor (female, male or combined sexes when the tooth wear data extracted from the study was not sex-specific), and taxonomy as a three level fixed factor (cervids, bovids or others). We also included species as a random factor to avoid pseudo-replication problems (sensu Hurlbert, 1984) because we had multiple values per species. Fitting species as a random effect was justified because tooth wear was normally distributed across species and allowed us to assess how much variation in tooth wear was accounted for by between-species differences. To account for allometry, body mass was analysed on a log-scale (Houle et al., 2011). Based on preliminary analyses indicating no evidence for two-way interactions between factors, we only analyzed the main effects. We selected models based on the Akaike's Information Criterion (AIC). We calculated AIC weights (w_i) to assess the relative likelihood of each model being the best among all the fitted models (Burnham and Anderson, 2002) and selected the model with the lowest AIC as the final model. When the difference between the AIC values (denoted ΔAIC) of two competing models was within two units, we retained the simplest model to satisfy parsimony rules, but we explored all terms within the set of models with ΔAIC within 2 units. Model coefficients (± SE) were obtained from the best model (i.e. bolded) presented in Table 1, but when otherwise specified.

2.2.3. Relationships between tooth wear, tooth height and age-specific change of survival

We assessed whether the intensity of tooth wear is associated with longevity and the intensity of actuarial senescence by replicating our analyses for longevity and our two metrics of actuarial senescence (i.e. rate of senescence and Gompertz rate). In all cases, we used linear mixed models using the senescence metric as the dependent variable and tooth wear, body mass (log-transformed) and diet (to correct for the higher senescence rate of browsers in captive populations) as independent continuous covariates, sex as a three level fixed factor (female, male or combined sexes), taxonomy as a three level fixed factor (cervids, bovids or others) and species as a random factor. We looked for main effects and also for the two-way interaction between sex and tooth wear to assess the possibility of between-sex differences in the association between tooth wear and actuarial senescence or longevity. Model selection was based on AIC and we selected the model with the lowest AIC as the final model. When the difference between the AIC values (denoted ΔAIC) of two competing models was within 2 units,

we retained the simplest model to satisfy parsimony rules, but we explored all terms within the set of models with ΔAIC within 2 units. We investigated potential changes in the association between senescence metrics or longevity and tooth wear induced by hypsodonty by including additive effects of tooth height. When the Gompertz rate was the dependent variable, models were corrected for the onset age of senescence as there is a strong correlation between these variables ($r = 0.52$; $t = 3.69$; $p < 0.01$). The onset age of senescence was estimated from the best Gompertz model. In the analyses involving longevity and actuarial senescence, we removed three species for which we did not have age-specific data on mortality: common duiker, *Sylvicapra grimmia* (Wilson et al., 1984), Japanese serow, *Capricornis crispus* (Miura and Yasui, 1985) and white rhinoceros (Hillman-Smith et al., 1986).

Since we had only a small number of closely related species, we did not correct for possible confounding effects of shared ancestry (see Saether et al., 2013 for a similar approach). All analyses were performed using R (version R.3.2.0) and the package lme4 (with the function lmer, Bates et al., 2015). Parameter estimates are given ± SE.

3. Results

3.1. Factors associated with tooth wear

The model selected for describing variation in tooth wear observed across populations of large herbivores included a random effect of species and a fixed effect of tooth height (Table 1, see Table S3 for a full account of model selection). As expected, from this model, tooth wear increased with tooth height (slope of 0.619 ± 0.232 on a log-log scale, Fig. 1). The among-species variation accounted for 85% of the total variation observed in tooth wear. The second best model included additive effects of body mass. For a given tooth height, tooth wear tended to decrease with increasing mass (slope of -0.275 ± 0.168 on a log-log scale). We did not find any support for differences in tooth wear between sexes or among families. Although the model including sex was within 2 AIC units, its AIC was higher with a larger number of parameters, which led this model not to be competitive. Only a slight trend for higher tooth wear for a given tooth height occurred for males (a difference of 0.198 ± 0.149). This effect seemed unimportant because the confidence interval around the coefficient widely overlapped zero.

3.2. Relationships between tooth wear, tooth height and age-specific change of survival

The model selected for longevity included a random effect of species and the fixed effect of body mass, in addition to the effect of diet that is included to correct for the effects of captivity on longevity (Table 1, see Table S4 for a full account of model selection). From this model, the among-species variation accounted for almost all (99.3%) of the total variation observed in longevity and, surprisingly, longevity decreased with increasing body mass (slope of -0.564 ± 0.047 on a log-log scale); this may be an artifact of captivity as that large species are probably more difficult to maintain in captivity than smaller ones. However, previous comparative analyses of survival metrics in captive populations did not detect any evidence for such an artifact (e.g. Lemaître et al., 2013; Tidière et al., 2014). While the models including additive effects of tooth wear had close AIC values (ΔAIC = 0.90, Table S4), the AIC value was higher for the more complex model and these effects were weak (slope of -0.302 ± 0.295). Longevity did not decrease markedly with increasing tooth wear. Neither family nor sex affected longevity. On a log-scale bovids had a longevity of only 0.265 ± 0.504 longer than cervids for a given body mass. Moreover, females had a longevity of only 0.042 ± 0.052 (log-scale) longer than males for a given body mass. The association between tooth wear and longevity for a given tooth height was also weak (slope of 0.065 ± 0.077, on a log-log

Table 1

Analysis of the possible factors associated with tooth wear, longevity, rate of actuarial senescence (measured as the proportional decrease of survival between 6 and 12 years of age), and Gompertz rate of actuarial senescence (corresponding to the exponential rate of mortality increase with age) in large herbivores. Species (SP) is included as a random effect, Sex (S: female, male or both sexes) and Family (F: Bovidae, Cervidae or others) as fixed factors and body mass (BM) and Diet (D) as covariates. Tooth height (TH) was also included as a covariate for tooth wear, and tooth wear (TW) was included as a covariate for longevity, rate of actuarial senescence between 6 and 12 years of age, and Gompertz rate of actuarial senescence. For longevity and the two metrics of actuarial senescence, tooth height was added to the selected model (no measure of w_i). We used AIC and AIC weight (w_i) to compare models. More information on both variables and analyses are available in the Materials and Methods section. The selected model is in bold. K represents the number of parameters. These analyses are based on 21 species and 66 independent measures for tooth wear, 17 species and 61 independent measures for longevity and rate of actuarial senescence between 6 and 12 years of age, and 13 species and 37 independent measures for Gompertz rate of actuarial senescence. The models displayed correspond to the selection of the best fitted models, which occur in grey in Tables S3 to S6 reporting all models tested for tooth wear, longevity, rate of actuarial senescence between 6 and 12 years of age, and Gompertz rate of actuarial senescence, respectively.

	k	AIC	ΔAIC	w_i
Tooth wear				
SP + BM + TH	5	119.58	0.00	0.31
SP + TH	**4**	**120.35**	**0.77**	**0.21**
SP + S + BM + TH	7	120.86	1.28	0.16
Longevity				
SP + BM + D	**5**	**−37.08**	**0.00**	**0.21**
SP + TW + BM + D	6	−36.18	0.90	0.13
SP + S + D	6	−36.08	1.02	0.12
SP + S + TH	6	−35.88	1.21	-
SP + S + TW + D	7	−35.84	1.25	0.11
Actuarial senescence rate (measured as the proportional decrease of survival between 6 and 12 years of age)				
SP + F + D + TW	11	−127.00	0.00	0.19
SP + F + D + S*TW + TH	12	−126.65	0.35	-
SP + F + BM + D + S*TW	12	−126.35	0.64	0.14
SP + F + S + D	8	−125.72	1.28	0.10
SP + BM + D	**5**	**−125.62**	**1.38**	**0.09**
SP + BM + D + TH	6	125.58	1.42	-
SP + F + D + S + BM	9	125.19	1.80	0.08
SP + S + D	6	125.01	1.99	0.07
Gompertz rate of actuarial senescence (exponential rate of mortality with age)				
SP + O + D + BM + S*TW	**11**	**−103.40**	**0.00**	**0.40**
SP + O + F + D + BM + S*TW	13	−102.34	1.06	0.24
SP + O + F + D + S*TW	12	−101.70	1.69	0.17
SP + O + D + BM + S*TW + TH	12	−101.52	1.87	-

scale), so variation in tooth height was not associated with variation in longevity.

Both metrics of actuarial senescence were positively correlated in both sexes (although very weakly and without any statistical support in males, Fig. 2). The clear relationship for females and the widely scattered measures for pooled sexes tracked quite well the quality of data. Indeed, sample sizes are usually larger for females than for males and not accounting for sex differences introduces heterogeneity that decreases the reliability of age-specific survival estimates in studies of pooled sexes.

The selected model of variation in the rate of senescence between 6 and 12 years of age included a random effect of species and the fixed effect of body mass, in addition to the effect of diet that is included to correct for the effect of captivity on the rate of actuarial senescence (Table 1, Table S5 for a full account of model selection). From this model, the among-species variation accounted for almost all (98.85%) of the total variation observed in the rate of senescence between 6 and 12 years of age and this rate of senescence, surprisingly, increased with body mass (slope of 0.166 ± 0.024). However, the model including additional effects of family (with bovids tending to have higher senescence rate than cervids by 0.248 ± 0.145) and of interactive effects between sex and tooth wear had the lowest AIC (Table S5). In particular, from this model, the rate of senescence increased with tooth wear much faster in males than in females (with a difference in slope of 0.794 ± 0.320). The increase approached statistical significance in
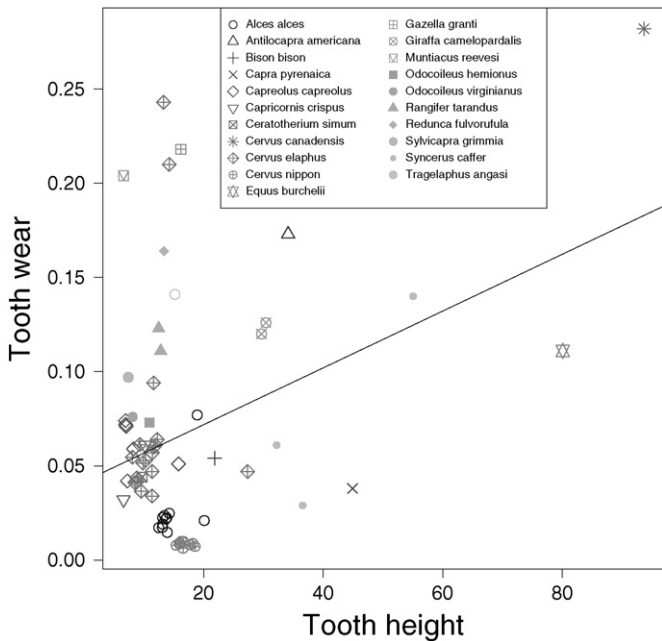
Fig. 1. Relationship between the tooth wear index and tooth height at the onset of actuarial senescence across populations of large herbivores. The tooth wear index was measured as the population and sex-specific slopes of the regression between log M1 height and age. The tooth height variable was estimated from the best Gompertz model for a given population and a given sex. The figure displays the raw data and the line of best-fit without correcting for between-species differences.

covariates, family as a fixed factor and an interaction between sex and tooth wear) on a dataset restricted to studies in which sex-specific measures of tooth wear were available confirmed this pattern of no detectable increase of senescence with increasing tooth wear in both males and females (e.g. slope of -0.247 ± 0.221 in females) and of an increasing senescence in males relative to females with increasing tooth wear (with a between-sex difference in slope of 0.521 ± 0.273). When an association between tooth wear and rate of actuarial senescence for a given tooth height was sought from the same model with an additive effect of tooth height, the patterns were reinforced. For a given tooth height, actuarial senescence was not associated with tooth wear in females (slope of -0.168 ± 0.300) but increased with tooth wear in males (slope of 0.55 ± 0.25), also leading the difference between these two trends to be statistically significant (a difference in slope of 0.725 ± 0.330, Fig. 3). Variation in tooth height was not associated with this rate of senescence (slope of -0.059 ± 0.053).

The selected model of variation in Gompertz rates across populations of large herbivores with the lowest AIC (Table 1, Table S6 for a full account of model selection) included an interactive effect between tooth wear and sex, fixed effects of the onset of actuarial senescence and of body mass, and a random effect of species, in addition to the effect of diet that is included to correct for the effect of captivity on Gompertz rates. From this model, the among-species variation only accounted for 15.9% of the total variation observed in Gompertz rate. As expected, the Gompertz rate increased with the onset of senescence (slope of 0.033 ± 0.009). While Gompertz rates at low tooth wear were lower in females than in males (difference of 0.079 ± 0.031), they strongly increased with tooth wear in females (slope of 0.916 ± 0.385; Fig. 4), whereas there was no relationship between tooth wear and Gompertz rate in males (difference of slope of -1.197 ± 0.435, Fig. 4). An analysis restricted to studies in which sex-specific measures of tooth wear were available confirmed this pattern (the results are available from the authors upon request). Gompertz rates were slightly influenced by variation in body mass (slope of -0.0193 ± 0.0132) and taxonomic grouping (difference of 0.054 ± 0.042 in favour of bovids compared to cervids). The associations between tooth wear and

males (slope of 0.418 ± 0.221), whereas in females, the trend was reversed with the rate of senescence in females showing a weak decrease with increasing wear (slope of -0.295 ± 0.244). Fitting the same model (i.e. species as a random effect, body mass and diet as
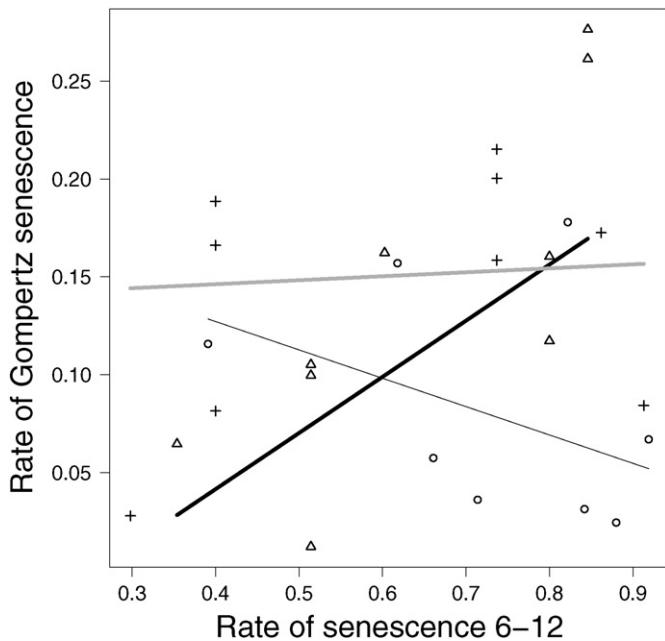

Fig. 2. Relationship between the rate of actuarial senescence (measured as the proportional decrease of survival between 6 and 12 years of age) and the Gompertz rate (measuring the exponential increase of mortality with age) across populations of large herbivores (males: plus sign and thick grey line, females: triangles and thick black line, pooled sexes: circles and thin black line). The figure displays the raw data and the best-fitting line for each sex category, with no correction for between-species differences.
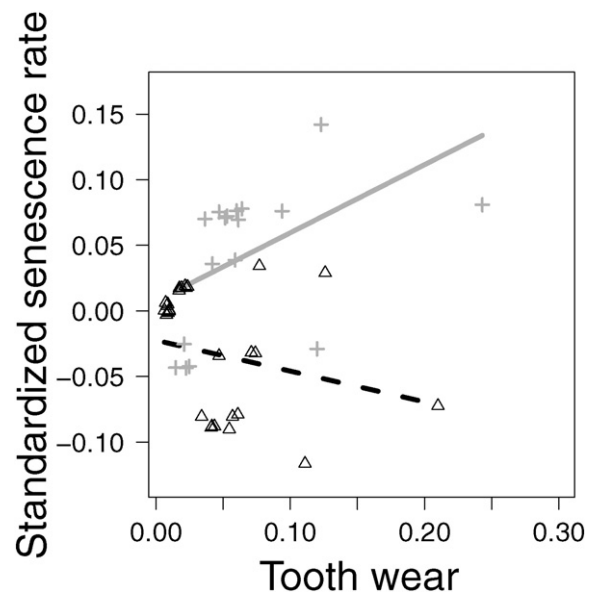

Fig. 3. Sex-specific relationship (males: plus sign and grey line, females: triangles and dotted line) between the rate of actuarial senescence between 6 and 12 years of age (measured as the proportional decrease of survival between 6 and 12 years of age) and the tooth wear index (measured as the population-specific slope of the linear regression between log-transformed tooth height and age). The figure displays the predicted values from the selected models (lines) and the partial residuals from the model accounting for all main effects but not the interaction between sex and tooth wear (data points). Dotted lines indicate trends that are not statistically significant.
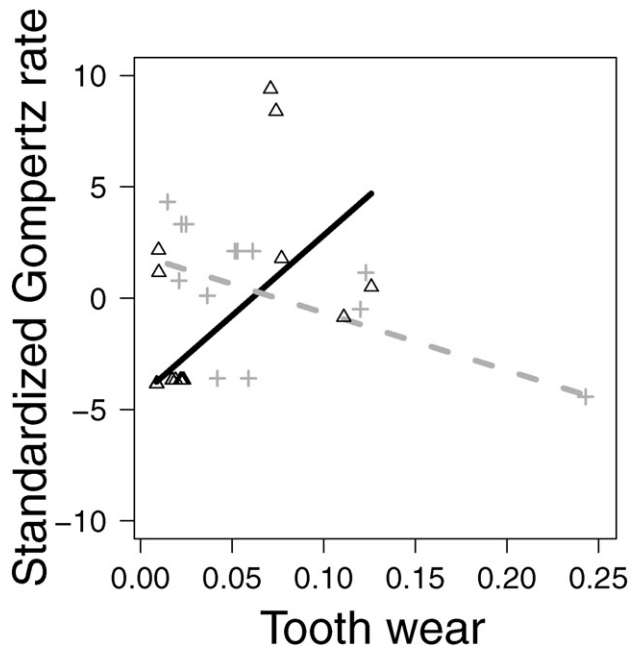
Fig. 4. Sex-specific relationship (males: plus sign and grey dotted line, females: triangles and full line) between the Gompertz rate of actuarial senescence [standardized for between-species differences (included as a random effect), adult body mass (included as a covariate) and diet (included as a covariate using the proportion of grass in the diet)] and the tooth wear index (measured as the population-specific slope of the linear regression between log-transformed tooth height and age). The figure displays the predicted values from the selected models (lines) and the partial residuals from the model accounting for all main effects but not the interaction between sex and tooth wear (data points). Dotted lines indicate trends that are not statistically significant.

Gompertz rates of senescence for a given tooth height showed the same patterns, so variation in tooth height was not associated with the strength of senescence (slope of 0.002 ± 0.034). For a given tooth height, actuarial senescence strongly increased with tooth wear in females (slope of 0.948 ± 0.406) and was independent of tooth wear in males, leading the difference between sex-specific slopes to be statistically significant (a difference in slope of -1.226 ± 0.448).

4. Discussion

We found that the variation in a standardized metric of tooth wear rates (i.e. the slopes of the regressions of the log-transformed M1 crown height on age) across species of large herbivores was positively associated with hypsodonty, as in Damuth and Janis (2014). Although no other association was supported, the tendency for associations we found between tooth wear and either body mass or sex were both in the expected direction. The weak between-sex differences we reported are in line with previous species-specific studies, which reported either higher tooth wear in males (like in red deer, Loe et al., 2003 in Norway, Carranza et al., 2004 in Spain) or no between-sex differences (Stirling, 1969 on Weddell seal, Veiberg et al., 2007a for roe deer). Further studies, including a broader taxonomic range, will be required to assess how variation in sex, mass, and taxonomy are associated with tooth wear more accurately. Nevertheless, our results clearly demonstrate that tooth wear differs markedly among species of large herbivores, both in the absolute sense and for a given hypsodonty.

When assessing the relationship between the intensity of tooth wear and actuarial senescence, it seems at first sight that the choice of the metric of actuarial senescence matters. When considering longevity or rate of senescence between 6 and 12 years of age, we did not detect any association with tooth wear and among-species differences accounted for most of the variation observed in these metrics. On the other hand, when measuring actuarial senescence using the Gompertz

rate, between-species variation was quite low and the association between tooth wear and senescence differed markedly between sexes. However, a detailed examination of the results shows that the overall pattern went in the expected direction: longevity tended to decrease with increasing tooth wear, the rate of actuarial senescence tended to increase with tooth wear when the sexes were pooled, and the Gompertz rate of senescence in females increased with tooth wear (although this relationship did not occur in males and even tended to be reversed). Likewise, as expected, females had lower Gompertz rates than males at low tooth wear (i.e. early ages). On the other hand, the association between senescence metrics and longevity with body mass was in the opposite direction compared to our expectation: longevity decreased and the rate of senescence increased with increasing body mass. Including an interaction between sex and mass to account for possible confounding effects of large sexual size dimorphism in most large herbivores (Weckerly, 1998) and faster senescence in males than in females (Clutton-Brock and Isvaran, 2007; Lemaître and Gaillard, 2013), or accounting for hypsodonty did not alter this negative association (results not shown). We cannot offer an interpretation of this result and further analyses on extended datasets will be required to clarify the pattern. Females tended to outlive males in terms of longevity at a given rate of tooth wear. When the rate of actuarial senescence between 6 and 12 years of age was considered, the same pattern of strong species differences and body mass variation associated with the rate of senescence occurred, as observed when longevity was the focal metric. However, while the linear effect of tooth wear on the rate of senescence did not differ statistically from 0 in either males or females, the rate of senescence was consistently higher in males than in females and a statistically significant interaction showed that between-sex differences increased with increasing tooth wear.

These findings were unchanged when tooth height was controlled for, which provides support for the scenario in which the rate of tooth wear is interpreted as a clue for general deterioration with ageing within a species. Between-sex differences in actuarial senescence when tooth wear is high are less easy to interpret and went in opposite directions depending on whether actuarial senescence was measured as the rate between 6 and 12 years of age or as the Gompertz rate. A mismatch in the timing of measures between senescence rates and Gompertz rates could account for such a discrepancy, as senescence rates were consistently estimated between 6 and 12 years of age, whereas both Gompertz rates and tooth wear were measured over the same age range, which varied across populations, so the pattern obtained using the Gompertz rate may be more accurate. Based on that metric, females exhibited higher actuarial senescence than males at high tooth wear. This finding is a bit surprising at first sight, but may be due to the effects of female reproduction. Indeed, lactation requires large amounts of calcium and magnesium, which competes with allocation of these nutrients to teeth (Laine, 2002). Repeated lactation events may therefore lead to increased tooth wear. Cumulative reproductive costs of lactation, the most energy and nutrient demanding reproductive stage in mammals (Sadleir, 1984; Clutton-Brock et al., 1989), have been reported to increase actuarial senescence, which fits the disposable soma theory (Lemaître et al., 2015). As a higher Gompertz rate at a given intensity of tooth wear is associated with later onset of senescence, the relatively strong senescence of females at high tooth wear occurs at quite old ages. A stronger association between tooth wear and senescence at old ages after several breeding attempts was also found in a study of female reindeer (Kojola et al., 1998).

The lack of strong association between the magnitude of actuarial senescence and tooth wear could result from potential confounding effects of environmental variation. While we accounted for environmental noise when measuring longevity and the senescence metrics by relying upon high quality data from captive populations (corrected for the confounding effect of diet, Müller et al., 2010; Lemaître et al., 2013), we were not able to do so when measuring tooth wear. Diet in captive populations strongly differs from diet in the wild, leading to

marked differences in the magnitude in tooth wear between wild and captive large herbivores (Kaiser et al., 2009). As diet in captivity does not reflect the type of diet a given species has adopted along its evolutionary history, we had to rely on tooth wear measured in the wild. However, for a given species, tooth wear can vary tremendously in relation to habitat conditions (e.g. Garrott et al., 2003; Veiberg et al., 2007a). Although we partly accounted for such intra-specific variation by including multiple populations for some species, the large amount of intra-specific variation in tooth wear was likely to mask at least partially the relationship between tooth wear and senescence. Further studies ideally performed at the individual level would allow more accurate investigation of how tooth wear is associated with actuarial senescence.

Our findings provide preliminary support for the expected positive relationship between the strength of actuarial senescence and the intensity of tooth wear across species of large herbivores, independently of whether tooth height was controlled for or not. Although the strength of the association varied according to sex and to the metric used for assessing actuarial senescence, this result suggests that hypsodonty does not mitigate the effects of tooth wear on survival completely. Further studies should focus on the possible factors mediating tooth wear and actuarial senescence. For example, there is evidence that wild ungulates suffer from senescence in body mass (Nussey et al., 2011) and such a decline, likely to reflect a loss of body condition, might possibly be a direct consequence of tooth wear, which could also make individuals more prone to a range of diseases. Finally, our comparative analysis highlights the fact that the relationship between actuarial senescence and tooth wear differs markedly between the sexes, perhaps due to the costs of reproduction in females.

Acknowledgments

Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.exger.2015.09.008.

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