Disposable-soma senescence mediated by sexual selection in an ungulate

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Senescence may result from an optimal balance between current reproductive investment and bodily repair processes required for future reproduction[1], a theoretical prediction difficult to prove especially in large, long-lived animals. Here we propose that teeth that have fixed dimensions early in life, but that wear during chewing, can be taken as a measure of total lifetime 'repair', and their wear rate as a measure of current expenditure in performance. Our approach also considers the sexual selection process to investigate the advance of senescence in males compared with females, when selection favouring competition over mates reduces the reproductive lifespan of males[2]. We studied carcasses of 2,141 male and 739 female red deer (*Cervus elaphus*) of different ages, finding that male molariform teeth emerged at a far smaller size than expected from body size dimorphism. This led to higher workload, steeper wear rate and earlier depletion of male teeth than in females, in concordance with sex-specific patterns of lifetime performance and reproduction. These findings provide the empirical support for the disposable-soma hypothesis of senescence[3], which predicts that investment in bodily repair will decrease when the return from this investment may not be realized as a result of other causes that limit survival or reproduction.

Senescence is defined as the progressive loss of function accompanied by decreased survival and reproductive rate with increasing age. Three main hypotheses have been proposed to explain how senescence may evolve: the mutation-accumulation hypothesis[4,5], the antagonistic pleiotropy hypothesis[6–8] and the disposable soma hypothesis[1,3,9]. In most cases, empirical data can hardly differentiate between them. For all three hypotheses, the evolutionary basis of senescence is the weakening of selection against the loss of function at older ages, because of lower survival or reproductive chances caused by extrinsic factors[7,10]. Experiments have been performed with short-lived organisms such as *Drosophila* and *Caenorhabditis elegans* to modify the extrinsic causes of survival or reproduction, with effects on the onset of senescence[8]. The experimental approach is less appropriate for investigating the causes of senescence in long-lived animals, for which comparison between populations may be an alternative. For birds and mammals, comparisons between populations revealed a relationship between extrinsic mortality before senescence and the rate of senescence[11]. However, the relationship between extrinsic mortality and senescence is common to all evolutionary explanations and cannot differentiate between hypotheses.

In studying the disposable-soma hypothesis, measuring body repair entails practical difficulties that hamper empirical support for the hypothesis. In red deer, as in most mammals, once the permanent teeth have erupted, the only changes to dentition are the gradual loss of teeth through wear. Although ungulate molars internally lay down secondary dentine, they cannot be repaired externally once worn. In many ungulates tooth wear has been shown to be a proximal cause of senescence[12–16]. A corollary of the disposable-soma hypothesis for teeth is therefore that they are produced with properties that allow the organism to use them during its expected reproductive lifespan.

We proposed that although selection in male red deer produced an increase in body size in comparison with females, it should have promoted only a slight increase in the size of teeth, because under the same selective process reproductive lifespan was reduced relative to that of females[2,17].

Maximum longevity recorded in our sample was 18 years for females and 13 years for males. On the basis of age distribution (Table 1), survival from age 2 years onwards followed log–log functions for males and females (male survival $= \exp(-\exp(0.76 - 0.22 \times \text{age}))$, $r = 0.987$, $N = 11$, $P < 0.0001$; female survival $= \exp(-\exp(0.85 - 0.15 \times \text{age}))$; $r = 0.974$, $N = 15$, $P < 0.0001$; see ref. 18). Accordingly, age-specific mortality rates fitted quadratic concave functions that were more pronounced in males than in females (for males, $y = 0.61 - 0.10x + 0.01x^2$, $r = 0.831$, $N = 12$, $P < 0.005$; for females, $y = 0.33 - 0.05x + 0.01x^2$, $r = 0.920$, $N = 12$, $P < 0.0002$; see also refs 17, 19, 20).

Plots of body mass against age followed quadratic convex functions with maximum values at 6.9 years in males and at 11.8 years in females (Fig. 1a). The relationship between crown height of the mandibular first molar (M1) and age followed quadratic concave functions in males and females (Fig. 1b). Crown height and age-specific rates of tooth wear differed between the sexes (analysis of covariance for natural logarithm of crown height with age as a covariate: for effect of sex factor, $F = 27.22$, d.f. 1, 2611, $P < 0.0001$; for interaction between sex and age, $F = 100.25$, d.f. 1, 2611, $P < 0.0001$; see also ref. 16). Even though males at 2 years of age started with slightly higher crowned first molars (11.0 mm compared with 10.8 mm in females), they were depleted at a higher rate (average 1.08 mm per year between 2 and 12 years of age) than in females (average 0.62 mm per year between 2 and 18 years of age) and, as a consequence, the absolute crown height of males (that is,

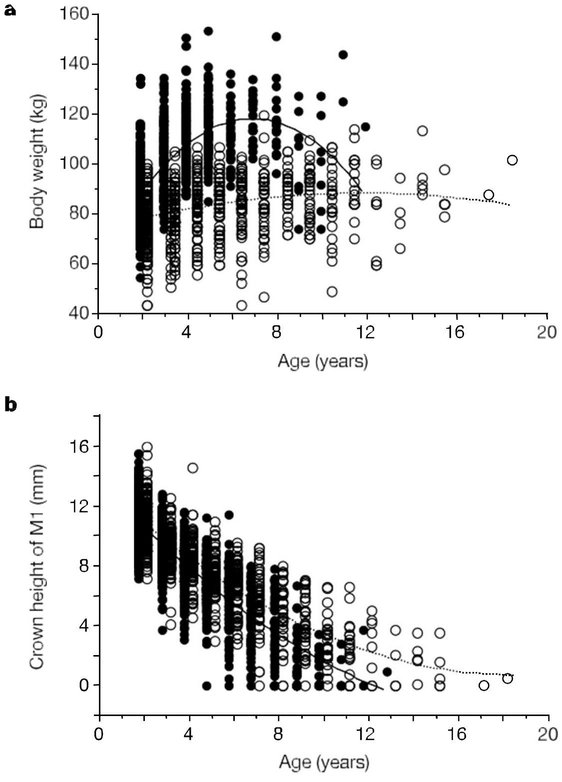

Figure 1 Performance and tooth wear throughout life in males and females. a, Variation in body mass with age for males (filled circles) and females (open circles). b, Crown height of mandibular first molar (M1) with respect to age for males (filled circles) and females (open

circles). For details of functions see Supplementary Information.

Table 1 Frequency distribution of males and females of different ages used in the study

Sex	Age (years)																
	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Female	196	125	93	69	66	50	36	36	25	19	8	4	5	5	0	1	1
Male	879	433	293	232	125	70	48	34	17	7	2	1					

The total number of males was 2,141; the total number of females was 739.

even without adjusting for differences in body size) was lower than that of females from 3 years of age onwards.

Standardized sexual dimorphism for variables denoting tooth size ranged from 0.87 to 1.12. By contrast, standardized sexual dimorphism for variables related to body size and body mass ranged from 1.16 to 1.48 (Fig. 2). The crown height of the second molar (M2) was a striking extreme case, even showing a slightly smaller size in males than in females. It should be noted that the low dimorphism among tooth dimensions was not a consequence of previous wear, because for structures that did not increase with age we used the measurements at 2 years of age (see Methods and Supplementary Information) when previous wear had been minimal or even non-existent for M2. Mean dimorphism for the five tooth dimensions (occlusal surface area (OSA) variables are derived from them) was significantly lower than body size dimorphism (1.04 ^ 0.10 s.d. compared with 1.34 ^ 0.11 s.d.; Mann–Whitney U: $z = 2.842$, $N_1 = 5$, $N_2 = 7$, $P = 0.005$, which did not depend on the extreme case; $P = 0.008$ after excluding M2). Dimorphism in all tooth dimensions lay below expectations from either isometric[21] or negative allometric[22] scaling with body size (Fig. 2). Although mandible size maintained an isometric degree of dimorphism, the postcanine tooth row (PCTR) did not match the expected increment in size (Fig. 2).

As molariform teeth wear, they experience changes that affect the working surface area. Particularly because of the mesio-distal flaring out of molars, wear affects the width of the crown very little but reduces its length. Consequently, M1 OSA decreased slightly with age. The length of the whole PCTR as well as the total OSA followed convex patterns but varied little with age (see Supplementary Information).

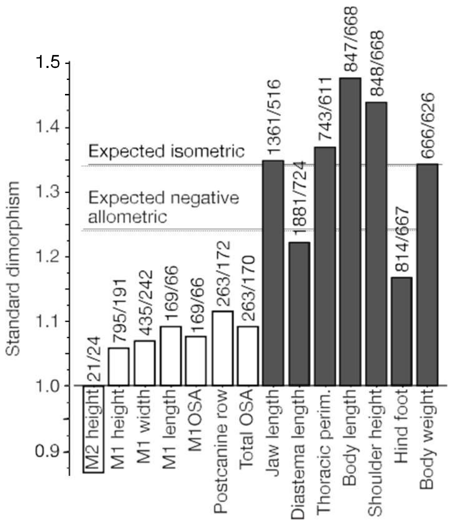

Figure 2 Sexual dimorphism (male/female ratio, standardized; see Methods), for different dental (open bars) and body size (filled bars) traits. Sample sizes (males/females) are indicated over the bars. Predicted standardized dimorphisms are shown, based on isometric (proportional to mass) and negative allometric (mass$^{0.75}$) assumptions.

According to current scaling theory[21,22], postcanine working surfaces should scale with (body mass)$^{0.66}$ (isometric assumption for surfaces[21]) or (body mass)$^{0.5}$ (negative allometric assumption for scaling surfaces with mass predicted by the mechanics of chewing[22]). We estimated individual workloads on postcanine working surfaces, dividing body mass taken to both scaling powers (0.66 and 0.5) by M1 OSA and total OSA (see Sup- plementary Information). In all age groups, male teeth supported a higher workload than female teeth (effect of sex in two-factor analyses of variance: for isometric assumption, M1 OSA: F 44.187, d.f. 1, 348, P ¸ 0.0001; total OSA: F 29.913, d.f. 1, 207, P , 0.0001; for negative allometric assumption, M1 OSA: F 24.978, d.f. 1, 348, P ¸ 0.0001; total OSA: F 15.988, d.f. 1, 207, P ¸ 0.0001).

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To maintain the same workload, the male/female ratio of dental working surfaces should match the male/female ratio of body mass taken to the scaling powers. Both the ratio of M1 OSA and that of total OSA were far below expectations, indicating that postcanine

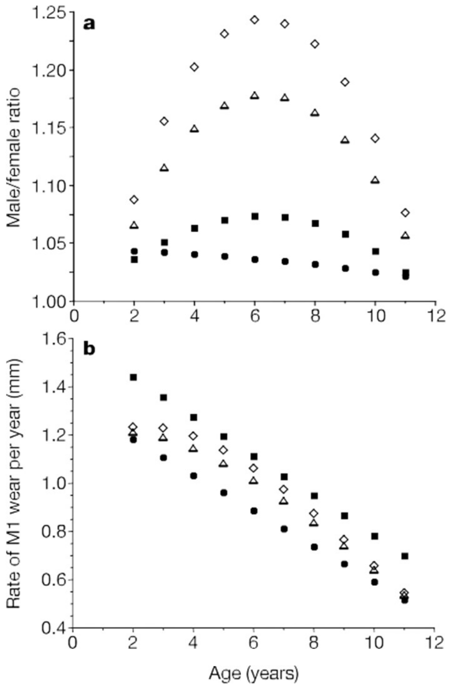

Figure 3 Postcanine working areas and wear. a, Expected male/female ratios for postcanine occlusal surface areas (OSA) according to isometric (exponent 0.66 for surfaces; open diamonds) and negative allometric (exponent 0.5, according to fracture scaling; open triangles) assumptions, and observed male/female ratios of total OSA (filled squares) and M1 OSA (filled circles) with age. b, Observed male (filled squares) and female (filled circles) wear rates, and predicted male wear rates based on both isometric (open diamonds) and negative allometric (open triangles) scaling criteria. These predictions were obtained by multiplying female rates by the ratio of expected to observed curves in a (using the observed M1 OSA because

occlusal surfaces of males were insufficient for the requirements derived from an increased body size in comparison with females (Fig. 3a).

To obtain a prediction of expected male M1 wear rate based on M1 relative size with respect to females, we corrected the pattern of M1 wear rate for females according to the ratio of M1 OSA relative to the expected ratio under both scaling criteria. Predicted male M1 wear rates were higher than female rates but did not reach the actual rates observed for males (Fig. 3b). This indicates that males are processing disproportionately more food than females, or food of lower quality[19,23–26], but also indicates that the size of male teeth should be positively allometric with respect to females to maintain durability. Predicted wear rates were closer to male observed values for prime ages (about 5–8 years). At younger ages, males depleted their dentine at a very high rate. A likely cause is the strategy of mass gain of males. Younger males experience a very high rate of body growth in comparison with females, and the difference between observed and expected wear was related positively to annual increment of body mass (from 2 to 6 years: $r = 0.940$, $N = 5$, $P = 0.017$; and $r = 0.950$, $N = 5$, $P = 0.013$, under both criteria respectively).

Sexual selection has moved red deer males towards a more semelparous schedule (about 6 years of reproductive lifespan) compared with females (about 14 years (refs 17, 19)). Our results clearly show that tooth size in males has been produced by selection to reach only the age above which reproductive chances are very low for causes other than tooth wear, which is strong evidence for planned senescence. Two main theories can account for the evolution of planned senescence: antagonistic pleiotropy[6] and disposable soma[9]. Distinction between them is frequently blurred because both concepts are founded on the idea of trade-offs between benefits in early and late life[1]. Antagonistic pleiotropy suggests that genes conferring positive benefits in early life may be favoured by selection even if they entail reproductive costs in later life. By contrast, disposable soma proposes that the trade-off between bodily use and repair is expected to lead to limited investments in the durability and repair of somatic structures. Therefore, although departures from optimal investment must also entail costs, the idea of early benefits and late costs is more fundamental to antagonistic pleiotropy, whereas planned durability is more compatible with disposable soma, thus providing a way of distinguishing between the hypotheses.

Possible early benefits of producing smaller teeth are to save materials and to accelerate tooth eruption. For materials, quantities seem too small to contribute significantly to skeleton or antler formation. For tooth eruption, M1 is already functional in both males and females at 1 year of age, and weaning is delayed in male calves[19]. In our data, although M1 thickness was smaller in males from 3 years onwards, the stained part of the M1 crown (see Methods) was higher in males until 4 years of age, indicating some delay in eruption compared with females. For possible costs in late life, depleted teeth are related to lower feeding efficiency[12,14–16,20], but this takes place in male red deer by the age of 11–12 years. Body performance starts to decline well before this age (Fig. 1), and probably also reproductive success, as indicated by data from other populations, once corrected for differences in longevity[17,19]. The smaller size of male M2 also supports disposable-soma predictions, because it erupted 1 year later than M1 and has to be used during an even shorter lifespan. Therefore, in the situation where males have evolved a significantly shorter reproductive lifespan arising from intrasexual competition over mates[2,17,19], the disposable-soma hypothesis[1,3,9] seems to be more appropriate for providing a ready explanation of why molars in this sex are under-provisioned for long-term function in comparison with females. Nevertheless, evidence in favour of the disposable-soma hypothesis is not opposed to antagonistic pleiotropy, but simply highlights how the mechanisms of somatic maintenance and repair have a role in the evolution of trade-off strategies underlying senescence[1].

We suggest that the comparison between sexes of dimorphic species for which the sexual selection process is well known opens up an interesting avenue of research, in which functional and proximal causes of the differences in reproductive patterns and senescence may be better understood than when comparing between species. In this context, the study of the features and wear rates of permanent teeth, or any other permanent structures, provide a promising field of evidence to explore how selection favours senescence. A

Methods

Red deer populations

Animals were 2,141 males and 739 females from 2 to 18 years of age, harvested in hunts in natural populations of Iberian red deer (*Cervus elaphus hispanicus*) in southwestern Spain. Thousands of stags are hunted every year in Spanish commercial hunts. Normally, every male deer aged 2 years or more can legally be shot. For females there are other non-commercial, management hunts aimed at reducing density, in which any female of any age can be culled, including calves. Hunting pressure on males is basically regulated by allowing only one hunting action per year in the same area and a minimum distance between hunters, whereas for females annual quotas are authorized by local government. In no instance did our study lead to the shooting of additional deer (for examples of use of harvesting data, see refs 16, 20, 27).

Recording of field data

Each hunting day we visited the place in the field where culled animals were gathered. From each animal we recorded some measurements in the field, and removed mandibles for further laboratory measurements. Field measurements were as follows: body mass of the complete animal (measured with electronic scales, 1–3 h after death, to the nearest 0.5 kg), body length (from nose to tip of tail excluding hair, following the dorsal body contour), shoulder height (from the vertebral column between the shoulders, the lateral contour along one foreleg, excluding the hoof), hind foot (straight length from the rear, outermost point of the hock to the beginning of the hoof) and thoracic perimeter (around the trunk behind the forelegs).

It was not possible to take all measurements for all individuals in the field, so numbers of samples for some measurements are smaller than the total number of animals recorded and are variable between measurements. For some hunting actions we had access to only the heads, not the whole bodies, which produced differences between sample sizes for head and body measurements.

Recording of laboratory data

Mandibles were used in estimating age and for taking measurements of jawbone and dental pieces, including wear. Age was estimated by counting cementum growth marks at the interradicular pad under the first molar[28], and checked by eruption patterns in younger animals. Ages are expressed in completed years from birth, so an animal aged n years is living its $n + 1$ year 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 in millimetres from the lowest point at mid-crown down to the central peak where the dentine touches the cementum layers. In some cases, the stained part of M1 crown height was measured from the disto-buccal cusp to the enamel/cementum line. For a subsample of individuals, we also measured crown height in the second molar (M2) as in M1.

From a sample of mandibles we took the following further measurements: jawbone length (the maximum straight line from the rearmost point of the ramus to the most distal part of the incisor alveoli excluding the incisors), diastema length (straight line between the lower incisor-shaped canine and the first premolar), PCTR (length of the PCTR of one ramus of the jaw (premolar + molar row) in individuals with the third molar erupted), M1 width (bucco-lingual diameter of the M1 occlusal plane), M1 length (mesio-distal diameter of the M1 occlusal plane), M1 OSA (width £ length of M1 occlusal plane) and total OSA (estimated as the product of PCTR and M1 width).

Data analyses

The proportion of survivors at age i was computed for individuals of age 2 years as the number of individuals of age i divided by the number of individuals of age 2. Age-specific mortality for age i was computed as 12[survivors at age($i + 1$)/survivors at age i]. Because mortality was estimated from transverse data, some cases of age-specific mortality of 0 or less occurred and were eliminated from the analysis because they have no biological meaning. Biased hunting might have affected only slightly our estimation of survival. Although some increase in mortality might be expected at age 2 years in males because hunting is allowed on stags from this age, our own experience with game managers indicates that culling intensity is not likely to vary for ages greater than 2 years. We can therefore safely assume that age-specific relative mortality at least for mature and older males is not dependent on hunting pressure, and the same applies to the maximum age recorded (which conforms to tooth wear data). The assumption of age-independent culling is safe for females, because they are culled simply to reduce density without any selective criteria.

Sexual dimorphism was measured as the size of a morphometric variable in males divided by that in females. To calculate dimorphism, we first fitted the relationship between trait values and age for males and females, and used maximum values of the curves for each sex. In particular, when relationships were decreasing linear or concave quadratic, we used mean values at 2 years of age; for convex quadratic relationships we used maximum values for male and female curves, and for asymptotic relationships we used the asymptotes.

Dimorphisms of linear measurements were standardized by elevating them to the third power and surfaces were multiplied by their square root, to make them comparable with volumes and weights. Dependent variables were explored for normality and homogeneity of variances. Crown height was transformed to ln(crown height + 1) to obtain linear relationships with age. The significance level was set at $P = 0.05$ and all P values are two-tailed.

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Competing interests statement The authors declare that they have no competing financial interests.