

The relationship between tooth wear, habitat quality and late-life reproduction in a wild red deer population

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Summary

1. Molar tooth wear is considered an important proximate mechanism driving patterns of senescence in ungulates but few studies have investigated the causes of variation in molar wear or their consequences for reproductive success.
2. In this study, we assessed molar tooth wear at death among red deer *Cervus elaphus* of known age on the Isle of Rum, Scotland.
3. First molar height showed a decelerating decline with age. In females, the rates of molar wear with age varied with location of home range and individuals experiencing low resource competition showed reduced molar wear. We suggest that this spatial variation in molar wear is related to differences in the availability of high-quality grazing habitat and levels of resource competition.
4. There was no evidence that females with more heavily worn molars had reduced reproductive performance late in life or that first molar height was associated with reproductive senescence.

Key-words: *Cervus elaphus*, habitat quality, local resource competition, molar tooth wear, senescence.

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Introduction

Senescence, defined as the progressive loss of organismal function with increasing age, is observed in the age-specific survival and reproduction patterns of numerous long-lived birds and mammals and has been documented in many wild ungulates (Gaillard *et al.* 1993; Loison *et al.* 1999). Ungulate body weight, survival, fecundity, and reproductive performance all show marked declines in old age (Bérubé, Festa-Bianchet and Jorgenson 1999; Loison *et al.* 1999; Myrsterud *et al.* 2001; Nussey *et al.* 2006). However, as yet relatively little attention has been paid to the proximate ecological mechanisms of ageing in these species. One frequently cited but rarely examined mechanism in ungulates is progressive wear and loss of function in the molar teeth (Skogland 1988; Gaillard *et al.* 1993; Kojola *et al.* 1998). Here, we assessed

patterns of molar tooth wear with age, its relationship with ecological conditions and consequences for late life fitness in a Scottish population of red deer *Cervus elaphus*.

The ability to obtain and process adequate food is essential to the maintenance of an individual's condition and hence their continued ability to survive and reproduce. In ruminants, it is particularly important that plant material is fully masticated in order that effective microbial digestion can occur (Skogland 1988; Gordon, Illius and Milne 1996). Although ruminant cheek teeth increase in height through the deposition of dental cement around their roots over time, the tooth surface cannot be repaired and constant grinding of plant material results in increasing levels of molar wear as animals age (Aitken 1975; Hewison *et al.* 1999; Carranza *et al.* 2004). Molar wear is thought to reduce the effectiveness of mastication and hence the amount of nutrition gained from ingested material (Skogland 1988; Kojola *et al.* 1998). It has frequently been postulated that heavily worn molars in late life represent a proximate mechanism driving senescence in reproductive traits and ultimately death, as individuals become

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increasingly unable to digest plant material effectively (Gaillard *et al.* 1993; Kojola *et al.* 1998). However, demonstrations of the fitness consequences of variation in tooth wear are extremely rare in mammals (although see King *et al.* 2005).

We know little about the ecological factors affecting tooth wear in ungulates. Individuals living in poor quality habitats, with low abundance of good quality grazing, may be forced to consume larger quantities of rougher, low quality forage types and thus increase rates of molar wear. For example, Kojola *et al.* (1998) showed that resource competition may affect tooth wear indirectly through its effects on the quality of available vegetation. High population densities may lead to a rapid depletion in available good quality food material, forcing animals to forage in lower quality habitats (Kojola *et al.* 1998). High grazing pressure will also lead to greens being cropped close to the ground, and feeding individuals may ingest more soil particles, leading to increased tooth wear (Skogland 1988; Loe *et al.* 2003). Evidence for density-dependent tooth wear in wild ungulate populations comes from comparison of separate populations experiencing different levels of resource competition (Kojola *et al.* 1998). Fine-scale variation in vegetation quality and resource competition is common in such systems (Clutton-Brock, Guinness and Albon 1982; Coulson *et al.* 1997) but tests of the effects of such fine-scale ecological variation on tooth wear in wild ungulate populations are lacking.

Tooth wear may also vary between the sexes. For example, in red deer there is evidence of faster rates of molar wear in males than females, and this has been explained in terms of intersexual differences in size and habitat preference (Loe *et al.* 2003; Carranza *et al.* 2004). In sexual dimorphic red deer, adult males require greater amounts of digested plant material to support their larger body weights. Increased rates of wear are expected to result from the increased mastication workload placed on male molars, as well as the tendency of adult male red deer to segregate on poorer quality habitat than females (Clutton-Brock *et al.* 1982; Carranza *et al.* 2004).

Studies examining the causes and consequences of molar wear in ungulates to date have typically utilized tooth measures taken from previously unidentified animals killed in annual culls (e.g. Kojola *et al.* 1998; Loe *et al.* 2003; Carranza *et al.* 2004). The life histories and habitat use of these individuals are largely unknown and, as a result, the fine-scale ecological correlates and fitness consequences of tooth wear cannot be tested. In this study, we examined the causes and consequences of molar tooth wear at death in a population of individually monitored red deer with known life histories on the Isle of Rum, Scotland. Molar height measures were taken from 524 lower jaws collected post-mortem from carcasses of individually recognizable deer that died of natural causes. Regular monitoring of this study population over a long time period means that life history and spatial data were available for most of these deer,

while population-wide and local demographic parameters are also known.

No study of ungulates, to our knowledge, has been able to relate fine-scale ecological variation to rates of molar wear or to test for relationships between molar wear and late-life reproductive performance (see von Hardenberg, Shipley and Festa-Bianchet 2003 for an example relating ungulate incisor morphology to fitness; King *et al.* 2005 for an example relating tooth wear to fitness in primates). Although the Rum study population represents a unique opportunity to address these issues, sampling from natural mortalities has drawbacks. In most ungulate systems mortality is highest in the first few years of life and in old age (Gaillard, Festa-Bianchet and Yoccoz 1998), and thus the sample will be biased towards the youngest and eldest age classes. Furthermore, the presence of associations between body size, tooth size at eruption and survival probability have the potential to bias estimates of tooth wear rates. The detailed individual-based nature of the Rum deer data set means that, in most instances, we were able to explore the potential roles of such biases in observed trends.

Our aims in this study were: (1) to describe patterns of molar wear with age in this population and assess differences between the sexes; (2) to assess the effects of resource competition and habitat quality on rates of molar wear in female deer; and (3) to determine if there is any evidence for a relationship between female reproductive investment and success in late life and the degree of molar wear.

Methods

STUDY POPULATION AND MEASUREMENTS

All data were collected on red deer in the North Block of the Isle of Rum, Scotland (a 12 km² study area located 57°01'N, 06°17'W). Individual-based monitoring of deer living in this area has been undertaken since the early 1970s. Deer resident to the North Block are recognizable as a result of natural idiosyncrasies or artificial markings (Clutton-Brock *et al.* 1982). Female red deer are strongly philopatric, and most individuals born in the North Block remain there throughout their lives (Catchpole *et al.* 2004). Since 1974, at least five North Block censuses have been carried out each month between January and May. Study area censuses consisted of observations along a set route during which the identities, locations (to the nearest 100 m² Ordinance Survey grid square), and groups of all deer observed were noted (Clutton-Brock *et al.* 1982). Reproductive histories of females were monitored through intense observation during the calving season (late May–June), during which about 80% of calves born in the study area were caught, weighed and marked. Mortality searches were conducted throughout the winter period (January–April) to locate carcasses of missing individuals that might have died. Complete life

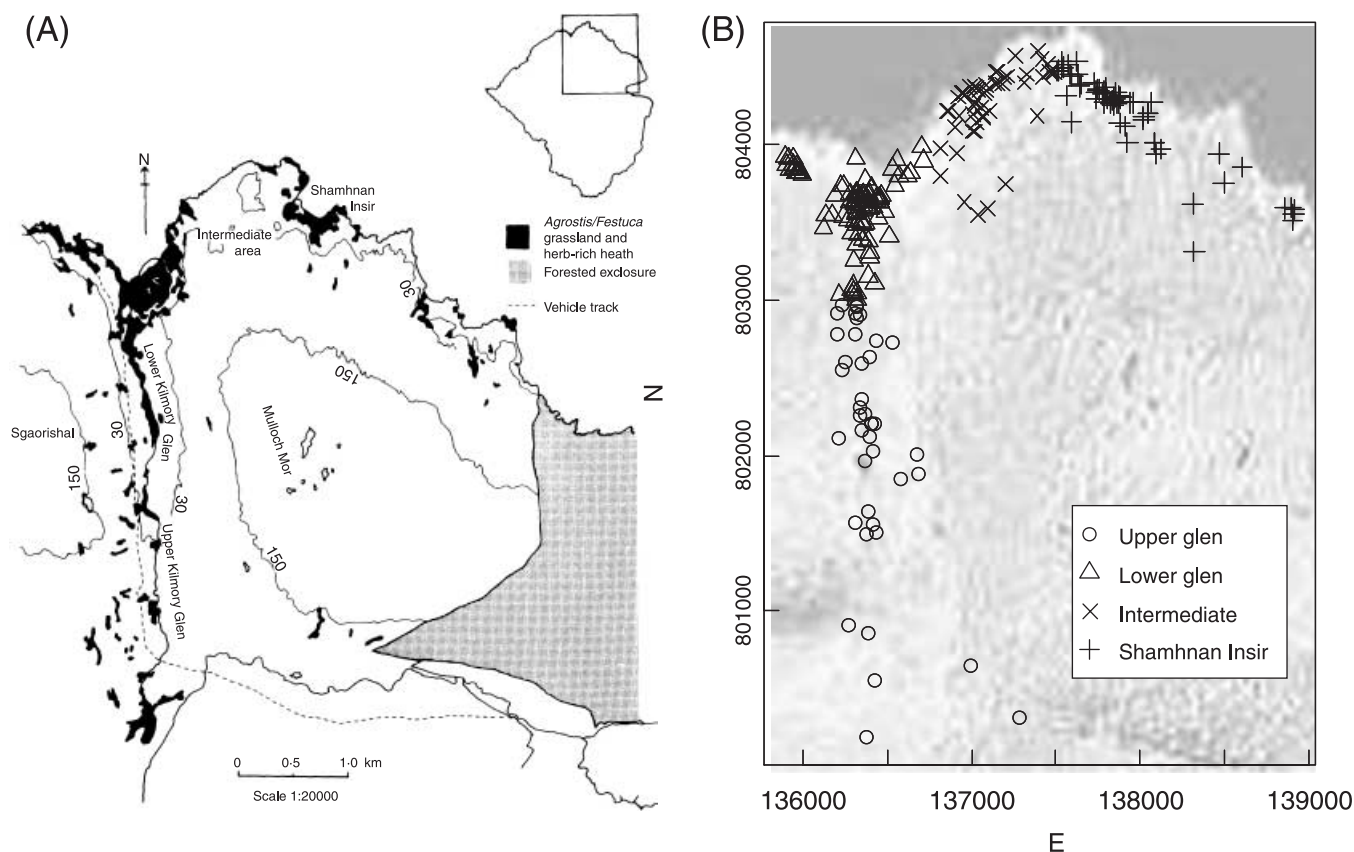


Fig. 1. (A) Map of North Block red deer study area with black shaded areas representing high-quality herb-rich grasslands. The study area's location with the Isle of Rum is highlighted in the inset map (reproduced from Guinness *et al.* 1978a). (B) The map shows centroid position of the home ranges of female red deer used in this study and illustrating the boundaries between the four population subdivisions used in the analysis presented here.

histories are known for the vast majority of females natal to the North Block study area, along with ecological and spatial data across their lifetimes.

Male red deer typically disperse beyond their mother's home range between the ages of 3 and 5, and many males born in the North Block move outside the study area's boundaries during this period (Clutton-Brock *et al.* 1982, 2002). Available life-history and spatial data for North Block males are therefore often complete only for the early part of their lives, although they remain recognizable and their carcasses are often found during mortality searches. Located male and female deer carcasses were identified and post-mortemed. The lower jaw of all individuals was removed, labelled and stored.

The ecological conditions experienced by deer resident to the North Block since the early 1970s have been temporally and spatially heterogeneous. Culling of deer within the North Block study area ceased in 1972 (Clutton-Brock *et al.* 1982). As a result, across the study period the number of resident adult female deer has increased, while there has been an accompanying decline in the number of adult males (Clutton-Brock *et al.* 2002; Coulson *et al.* 2004). The population is thought to have reached carrying capacity in the early 1980s and population size has fluctuated around 200 resident adult females since then (Clutton-Brock *et al.* 2002).

Vegetation in the North Block is predominantly comprised of *Molinia* and *Calluna* dominated heath and grassland, with herb-rich *Agrostis–Festuca* grassland concentrated in patches at the North of Kilmory Glen and in Shamhnan Insir bay (Fig. 1A). Previous work suggests that deer are found at highest densities at and around regions of *Agrostis–Festuca* grassland, as this represents the highest quality grazing habitat (Clutton-Brock *et al.* 1982). The North Block has been divided into four subdivisions based on similarities in vegetation and topography (Guinness, Albon and Clutton-Brock 1978a; Guinness, Clutton-Brock and Albon 1978b): Lower and Upper Kilmory Glen ('LG' and 'UG', respectively) in the west of the study area, Shamhnan Insir ('SI') in the north-east, and the intermediate area ('INT') between LG and SI (see Fig. 1B). The subdivisions vary substantially in the distribution and quantity of herb-rich *Agrostis–Festuca* grassland and in associated levels of local resource competition (Clutton-Brock *et al.* 1982). These differences are associated with spatial variation in calf mortality (Guinness *et al.* 1978b; Coulson *et al.* 1997), female reproductive parameters (Guinness *et al.* 1978a; Iason, Duck and Clutton-Brock 1986), kin spacing behaviour (Albon *et al.* 1992), female fitness and population growth (Conradt, Clutton-Brock and Guinness 1999; Milner-Gulland, Coulson and Clutton-Brock 2000).

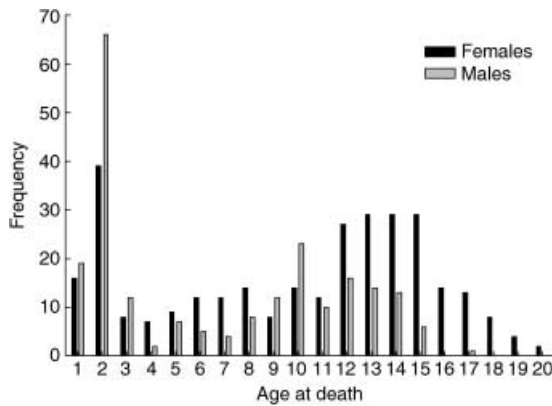


Fig. 2. Histogram showing sample sizes for measures of first molar height for males and females at each age of death.

Highest deer densities are found in the north of the study area (LG, INT, SI). The UG subdivision has had considerably lower deer numbers than other subdivisions throughout the study period (Coulson *et al.* 2004). LG is the area richest in good greens (Fig. 1A; Guinness *et al.* 1978b). SI contains concentrated regions of good greens around which most deer in the subdivision are usually seen. The INT and UG areas have little in the way of herb-rich greens (Fig. 1A), however, the small regions of *Agrostis-Festuca* grassland at the edges of INT are enriched by gull droppings and are thought to represent the most nitrogen-rich vegetation in the study area (Iason *et al.* 1986). Previous analysis suggests the subdivisions can be crudely ranked according to the availability of high-quality vegetation (LG > SI > INT > UG) and local population densities (LG > INT > SI > UG).

Although deer from the study area are occasionally shot outside its boundaries, most red deer in the North Block die of natural causes (Clutton-Brock *et al.* 2002). Here, we examined patterns of tooth wear among red deer dying of natural causes between 1974 and 2005. Our sample consisted of jaws with intact and fully erupted first molars (i.e. age at death ≥ 1 year) from 218 males and 306 females born in the North Block and aged 1–20 years at death (see Fig. 2 for sample sizes by age and sex). The height of the first molar is a commonly used index of wear in ungulates (e.g. Hewison *et al.* 1999; Loe *et al.* 2003). Height of the first molar (henceforth, 'M₁') was measured, using 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), following Loe *et al.* (2003).

In our analysis of ecological and life-history correlates and consequences of molar wear we used the following variables.

Age at death

Age was determined either through knowledge of an individual's year of birth or, for cases where females were born before monitoring began (7.5% of females in

our sample), from tooth cementum layers analysed post-mortem (see Clutton-Brock *et al.* 1982 for further details).

Cause of death

Most deer sampled died of starvation or exposure during winter ('natural winter mortality': 83% of females, 85% of males). Accidental deaths included falls or males killed in fights during the rut (4% of females, 9% of males). A small number of females died giving birth (6%). A further 7% of females and 6% of males sampled died of unknown causes, typically because their carcasses were found in a decomposed state some time after death.

Jaw length

Measured as the distance from the outer part of the fourth incisor socket to the posterior edge of the jaw (Kruuk *et al.* 2000). This was used as an indicator of individual body size (as in Loe *et al.* 2003).

Birth weight

More than 80% of calves born in the study area are caught shortly after birth and weighed. Birth weights were calculated based on weight at capture and hours since birth following Clutton-Brock *et al.* (1982). Birth weights were used as an indicator of early life body size and condition (Kruuk *et al.* 1999).

Subdivision

Each individual was allocated to one of four population subdivisions based on the location of the centroid of their home range (see Fig. 1B). Lifetime home range centroids were based on all January to May census records. This subset of censuses only considers times outside the rut and calving, as individual locations during these key periods in the breeding cycle of red deer may not be a good representation of an individual's foraging range (Coulson *et al.* 1997). Home range centres are commonly calculated by using the harmonic mean of the individual's range as this has been shown to be a close approximation of the true activity centre (Dixon and Chapman 1980). These mean positions were then allocated to one of each of the four subdivisions of the population (LG, UG, SI, or INT; see Fig. 1B). This was measured for females only.

To assess 'fidelity' of females to each subdivisions, we calculated the proportion of January to May census sightings in which each female was located within the boundaries of its allocated subdivision. Average proportions were taken for each subdivision.

Overall population density ('OPD')

The number of females aged 1 year or more that were seen in greater than 10% of January to May censuses of

that year (these were deemed to be resident adult females; Coulson *et al.* 1997). We used the OPD estimate from an individual's year of birth to assess the effects of early experience of population-wide levels of resource competition on tooth wear.

Local population density ('LPD')

This was estimated using hierarchical cluster analysis of female social groups identified during January to May censuses at the 96.5% level, as detailed in Coulson *et al.* (1997). Here we used the mean LPD across an individual's lifetime to assess the effects of experience of local competition on molar wear. This was measured in females only.

Offspring survival

This was scored according to whether a newborn deer survived until 1 May of the year following its year of birth ('1') or not ('0'), as this represents the period in which the majority of juvenile mortality occurs (Clutton-Brock *et al.* 1987).

Female reproductive status

A female's status, as categorized according to her reproduction in the previous year, has been shown to predict offspring birth weights and survival (Clutton-Brock *et al.* 1982). It was categorized as follows: (1) milk (female gave birth the previous year and her calf was still alive on 15 May of following year); (2) summer yield (gave birth the previous year and her calf had died before 1 October of that same year); (3) true yield (had not given birth the previous year); (4) winter yield (gave birth the previous year and the calf had died over the following winter – defined as between 1 October and 15 May).

STATISTICAL ANALYSIS

To describe changes in M_1 with age in male and female red deer we compared the explanatory power of additive models (AMs), which fit nonparametric smoothing functions to data, to polynomial linear functions of age (Venables and Ripley 1996). AMs have the advantage that they provide excellent descriptions of the relationship between two covariates without making assumptions about linearity. However, interactions between explanatory variables are less easily explored and tested in AMs than linear models (LMs) (Mysterud *et al.* 2001; Loe *et al.* 2003). We ran AMs for M_1 separately for males and females, using the default nonparametric smoothing function implemented in S-PLUS version 6.2 (Insightful Inc., Seattle, USA) and compared their explanatory power with LMs fitted with linear, quadratic and cubic polynomial functions (Venables and Ripley 1996).

Visual inspection of plots of AM smoothing functions suggested the changes in M_1 with age in both sexes

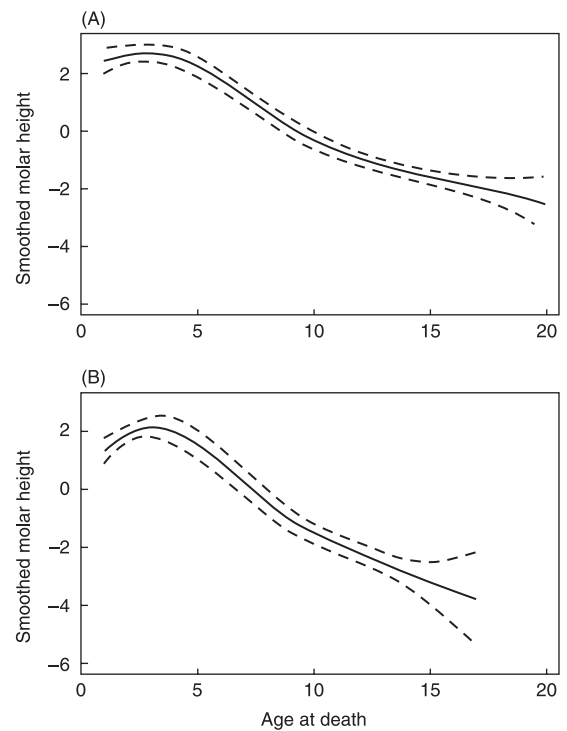


Fig. 3. Nonparametric smoothing functions, with dashed lines showing the standard error, from additive models of first molar height showing changes in first molar height with age at death in (A) female and (B) male red deer.

from 3 years onwards might be adequately described by a concave curvilinear relationship (see Results, Fig. 3). Such a relationship could be fitted using a quadratic term for age in a LM, and this was desirable as we wished to test the effects of ecological variables, and their interactions with age, on M_1 . AMs for each sex were re-run, including only deer that died at age 3 years or older. The explanatory power of these models was again tested against a LM fitted with a quadratic function of age. If the M_1 -age relationship was concave curvilinear, then it would be adequately described by a quadratic linear function and we would expect the AM function not to explain significantly more of the residual variance than a quadratic function of age.

We found that a concave curvilinear relationship from age 3 onwards adequately described the relationship between M_1 and age in both sexes (see Results). The residuals in LMs of M_1 were normally distributed. We tested for differences between the sexes using a LM of M_1 including data from all males and females aged 3 years or more at death with age at death, its square, sex and their interactions as explanatory terms. A significant main effect of sex would indicate differences between males and females in M_1 intercept, while interactions between sex and age or age² would indicate differences in the change in M_1 with age. This analysis was re-run excluding all deer that died in accidents or while giving birth to ensure cause of death was not biasing results.

Further analyses sought to assess possible sources of bias in our sample of M_1 measurements and, in particular,

the possibility that larger deer with larger or less worn molars were likely to survive to older ages. We used jaw length and birth weight as indicators of size. We restricted our analysis to deer that survived to 3 years of age as only these deer were the focus of detailed tooth wear analysis. We tested whether birth weight predicted jaw length using a linear model of jaw length including birth weight, with additional factors correcting for age at death and sex, including all available data on these two measures. The relationship between our two size measures and M_1 were assessed separately in each sex using a similar linear regression of size and age at death on M_1 . The relationship between birth weight and longevity was then also analysed for each sex by simple linear regression, using both the data set sampled and an expanded data set including all available data on animals of known year of death.

Our second aim was to explore fine-scale ecological effects on M_1 and its decline with age. As much less data were available for ecological conditions experienced during adulthood for males than females these further analyses were conducted on females only, again including only those dying at three or more years of age. We ran LMs of female M_1 including age at death and its square as main effects, along with measures of body size (jaw length and birth weight) where available. Spatial and ecological explanatory variables (population subdivision, LPD and OPD) were also fitted as well as all interactions of these variables with age at death. These LMs were simplified by dropping the term that explained the least residual variance and testing the significance of this model change by comparing models using the ANOVA command in S-PLUS (Crawley 2002). This process was continued until only those terms whose deletion from the model produced significant changes in the amount of residual variance explained ($P < 0.05$) remained. This final model was designated the minimum adequate model (MAM). The model was re-run excluding females that died in accidents or giving birth to test for bias due to different causes of death. We also tested for differences between female survival between subdivisions with LMs of age at death including female's subdivision as a factor, using both the restricted molar height data set used above and an expanded data set including all available females from the population of known age at death and subdivision.

Finally, in order to address the effects of the degree of M_1 wear on late life maternal fitness and provisioning ability, we required an age-corrected measure of M_1 for each female. We took residual first molar height (from a LM including all females that died at 3 years of age or later, with age at death and its square as covariates) and examined its effects on two important components of maternal fitness in this population: offspring birth weight and offspring survival through first winter (Clutton-Brock *et al.* 1987; Kruuk *et al.* 1999). Positive M_1 residuals indicate that a female had a large (unworn) first molar for her age at death, while negative M_1 residuals would indicate a relatively worn first molar for a female's age.

Molar wear was only likely to become a factor influencing an individual's ability to process food, and hence her ability to provision offspring, in late life (Kojola *et al.* 1998; King *et al.* 2005). We examined effects of residual M_1 on the maternal traits among females that died aged 12 or older. This seemed a sensible cut-off as the average age of death for females surviving to adulthood in this population is about 11 years old, and senescent declines in female reproductive traits has been observed in females from 11 years onwards (Guinness *et al.* 1978a,b). The birth weight and probability of survival of a female's last calf before she died within this subset of 'old' females was examined. In a handful of cases these females survived beyond the winter following their last breeding year (9%). The LM for last offspring birth weight included offspring sex and female's reproductive status as well as ecological variables (female's LPD, OPD, and population subdivision) and residual M_1 . A generalized linear model (GLM) for last offspring survival, with binomial error structure, was fitted including the same explanatory variables. Both models were re-run excluding females surviving beyond the year after last reproduction to ensure these females were not biasing results.

Results

CHANGES IN M_1 WITH AGE

The change in first molar height with age was nonlinear, but broadly consistent between the sexes (Fig. 3). There was a slight increase in M_1 from ages 1 to 3, which was more pronounced in males than females, followed by a decline in M_1 from age 3 onwards (Fig. 3). The AMs for both sexes explained more residual variance in M_1 than a cubic linear function of age (comparisons between AM and cubic LM: females: $F_{(d.f.=1)} = 16.27$, $P < 0.001$; males: $F_{(1)} = 11.61$, $P < 0.001$).

There was a decelerating decline in M_1 with age among both 251 sampled females and 133 sampled males of three or more years of age. This relationship was adequately described by a quadratic function of age at death: there was no significant difference between the explanatory power of an AM and a LM with a quadratic function of age in this subsample (females: $F_{(2)} = 1.88$, $P = 0.19$; males: $F_{(2)} = 1.41$, $P = 0.25$).

The rate of decline in M_1 with age did not differ between the sexes (Fig. 4). In the LM including data from both males and females aged 3 years or more, the interactions between sex and age at death and its square were not significant (effect of dropping both interactions from LM of M_1 : $F_{(2)} = 0.33$, $P = 0.72$). The main effect of sex revealed a marginally nonsignificant trend towards males having a slightly lower estimated M_1 at eruption (subsequently dropping sex from LM: $F_{(1)} = 3.55$, $P = 0.06$). The estimated effects of age on M_1 in the minimum LM were: age = -0.88 ± 0.09 SE, age² = 0.024 ± 0.004 SE, $F_{(2,381)} = 234.5$, $P < 0.001$ (see Fig. 4). Re-running the model excluding deer that died in accidents or giving

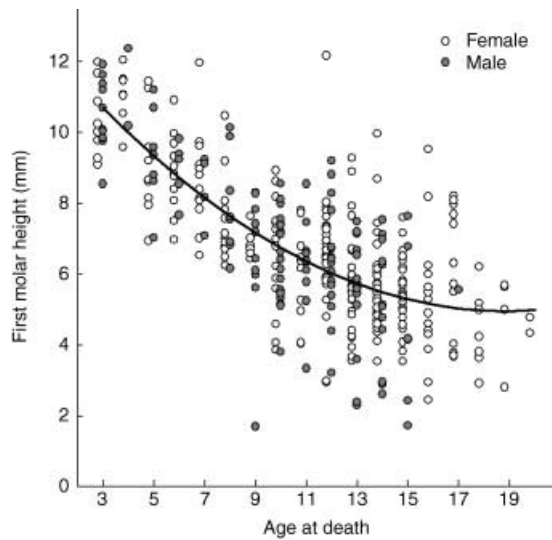


Fig. 4. First molar height plotted against age at death for females (empty circles) and males (filled circles) aged 3 years or older at death. The predicted quadratic effect of age on molar height, which was not significantly different between the sexes, is plotted.

birth did not affect these findings (age = 0.89 ± 0.10 , age² = 0.025 ± 0.005 , $F_{(2,330)} = 156.2$, $P < 0.001$).

There was no evidence for positive relationships between size, molar height and survival that might have biased these results. Our two size measures were positively associated, birth weight significantly and positively predicting jaw length (LM of jaw length including age at death and sex; birth weight: $F_{(1,647)} = 214.1$, $b = 2.41 \pm 0.61$ SE, $P < 0.001$). Among deer dying aged 3 years or more, neither jaw length nor birth weight predicted age-corrected M_1 in either sex – LMs of M_1 including age at death; (1) birth weight: females: $F_{(1,133)} = 0.30$, $b = 0.05 \pm 0.08$, $P = 0.58$; males: $F_{(1,200)} = 0.08$, $b = 0.003 \pm 0.011$, $P = 0.77$; (2) jaw length: females: $F_{(1,81)} = 0.70$, $b = -0.11 \pm 0.13$, $P = 0.41$; males: $F_{(1,97)} = 0.05$, $b = 0.004 \pm 0.018$, $P = 0.83$. Although the effect of jaw length on longevity could not be assessed because it was measured at death, we found no evidence that birth weight was positively associated with survival among animals aged 3 years or more in both our M_1 sampled data set (females: $F_{(1,148)} = 0.05$, $b = 0.06 \pm 0.28$, $P = 0.83$; males: $F_{(1,91)} = 0.24$, $b = -0.14 \pm 0.28$, $P = 0.62$) and in an expanded sample including all available animals of known age at death (females: $F_{(1,211)} = 1.27$, $b = 0.29 \pm 0.26$, $P = 0.26$; males: $F_{(1,141)} = 0.02$, $b = -0.03 \pm 0.23$, $P = 0.90$). A previous analysis has shown that birth weight influences future male, but not female, reproductive success in this population, but found no evidence for an effect of birth weight on longevity in either sex (Kruuk *et al.* 1999).

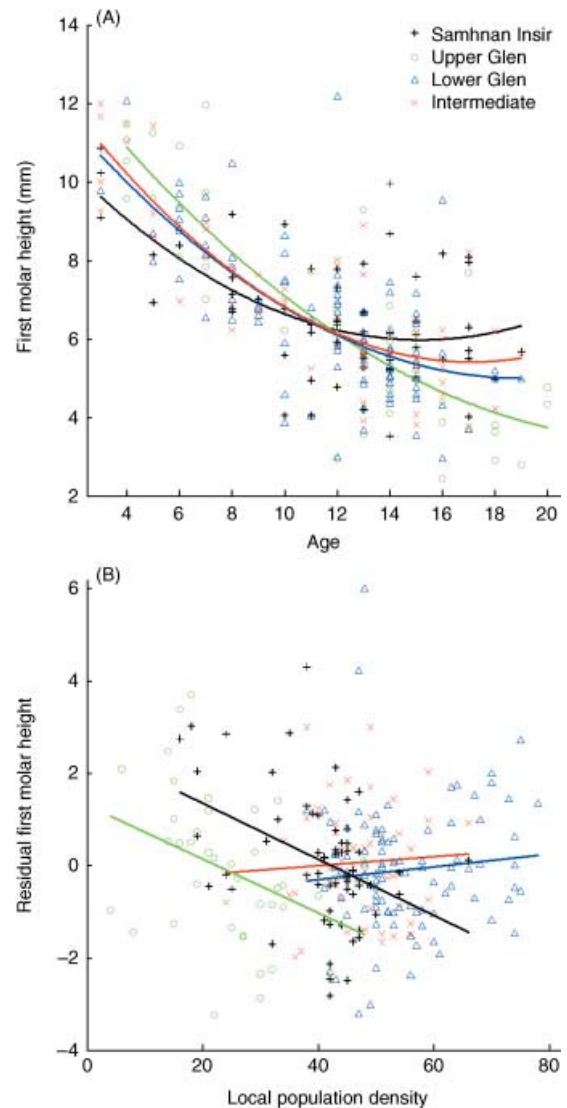


Fig. 5. Spatial heterogeneity in molar wear and the effects of local population density on first molar height. (A) First molar height plotted against age at death for females resident to different population subdivisions (see key). Least-squares regression lines using age and its quadratic are plotted through the data of each subdivision. (B) Residual (age-corrected) first molar height plotted against local population density experienced by females in each subdivision with regression lines through the data from each subdivision.

(Table 1; Fig. 5). The MAM of M_1 for females (Table 1) contained two significant interactions: (1) population subdivision by age ($F_{(3,236)} = 4.79$, $P < 0.01$), and (2) LPD by subdivision ($F_{(3,236)} = 3.50$, $P < 0.05$). There was no significant interaction between subdivision and age² (addition of subdivision by age² to MAM: $F_{(3)} = 0.20$, $P = 0.89$). This suggests that spatial variation existed in the rate of M_1 wear rather than the concavity of this decline. Furthermore, there was no evidence of a three-way interaction between age, subdivision and LPD (addition of interaction to MAM: $F_{(4)} = 1.04$, $P = 0.39$). Exclusion of females that died in accidents or giving birth from the model did not affect these results. The mean proportion of census sightings

ECOLOGICAL CORRELATES OF MOLAR HEIGHT AND WEAR RATES

In females, rates of M_1 wear and the effect of LPD on M_1 height differed between population subdivisions

Table 1. Minimum adequate linear model of first molar height among female red deer that died aged 3 years or more ($n = 251$). F and P -values are tested based on type III sums of squares. Main effects and interactions with subdivision are shown as the estimated effect and its standard error for the INT subdivision, followed by differences of each subdivision estimate from this effect and the standard error and significance of the difference. The interactions are illustrated in Fig. 5

Term	Estimate	SE	F	d.f.	P
Subdivision			3.37	3	< 0.05
INT	12.55	1.44			
vs. LG	-0.40	1.66			0.80
vs. UG	+3.09	1.5			< 0.05
vs. SI	+1.19	1.72			0.49
LPD			3.17	1	0.08
Age			60.44	1	< 0.001
Age \times subdivision			4.78	3	< 0.01
Age (INT)	-0.83	0.11			
vs. LG	-0.00	0.06			0.97
vs. UG	-0.13	0.06			< 0.05
vs. SI	+0.10	0.06			0.10
LPD \times subdivision			3.50	3	< 0.05
LPD (INT)	0.01	0.02			
vs. LG	+0.00	0.03			0.91
vs. UG	-0.06	0.03			0.07
vs. SI	-0.06	0.03			0.06
Age ²	0.02	0.00	20.80	1	< 0.001

Subdivision abbreviations: INT, Intermediate area; LG, Lower Kilmory Glen; UG, Upper Kilmory Glen; SI, Shamhnan Insir (see Fig. 1 for map).

of females within their allocated subdivision were generally high, with the exception of INT (INT: 0.53; LG: 0.84; UG: 0.70; SI: 0.90). There was no evidence for differences in longevity associated with subdivision either in the molar height sampled females ($F_{(3,246)} = 0.55$, $P = 0.65$) or for all females in the population ($F_{(3,641)} = 1.88$, $P = 0.13$).

A significant three-way interaction would indicate differences in the effect of LPD on rates of molar wear between subdivisions. The presence of an age by subdivision interaction in the MAM means that the LPD by subdivision interaction tests the effects of local density that are independent of subdivision-specific molar wear rates. Thus, it is evidence for a difference in the effect of LPD on age-corrected M_1 measures between subdivisions. Table 1 contains estimated effects of these interactions; Fig. 5 visually illustrates them using regression lines plotted through the raw or age-corrected M_1 data from females in each subdivision.

Female deer resident to the UG had a significantly faster rate of decline in M_1 with age than deer from other subdivisions (Table 1; Fig. 5A). SI females' M_1 wear rate was significantly slower than other subdivisions, while LG and INT had intermediate rates of decline in M_1 with age that were not significantly different from one another (Fig. 5A). Independent of a female deer's age at death, the effect of LPD on the height of her first molar varied between subdivisions: in areas with lower LPDs (SI and UG) increasing local densities were associated with more worn first molars, while in areas of generally higher resource competition (LG and INT) there was little effect of LPD on M_1 (Fig. 5B). Figure 5(B) shows the changes in residual

M_1 values (from a LM of M_1 fitted with age and age²) with LPD in each subdivision of the study area. The plot clearly illustrates that it is females living in SI and UG that experience the lowest lifetime LPDs, and that only among those females is increased resource competition (high LPD) associated with more worn M_1 values.

EFFECTS OF M_1 WEAR ON FEMALE LATE LIFE FITNESS

There was no evidence of significant effects of residual M_1 in late life on a female's ability to provision her offspring either during gestation or in early life. Residual M_1 was not significant in models of last offspring birth weight ($F_{(1)} = 1.29$, $b = -0.10 \pm 0.09$ SE, $P = 0.26$) and last offspring survival ($\chi^2_{(1)} = 1.24$, $b = -0.18 \pm 0.16$ SE, $P = 0.27$). All other terms in the models were also non-significant, with the exception of reproductive status, which significantly predicted both last offspring birth weight ($F_{(3)} = 8.37$, $P < 0.001$) and survival ($\chi^2_{(3)} = 10.06$, $P < 0.05$). Old hinds that were true yields had significantly larger offspring and those offspring were significantly more likely to survive their first year of life (see also Clutton-Brock *et al.* 1982, 1987). Excluding females that survived beyond the winter following their last reproductive attempt did not affect these results.

Discussion

First molar height showed a concave curvilinear decline with age from 3 years old among red deer in the North Block study population, and the rate of this decline was not significantly different between males and females.

In females, both population subdivision and LPD affected M_1 suggesting fine-scale spatial variation in habitat quality and resource competition may influence rates of tooth wear. There was no evidence that levels of first molar wear in females influenced either the birth weight or survival of offspring in late life.

CHANGES IN M_1 WITH AGE IN MALES AND FEMALES

The decelerating decline in M_1 with age among red deer in the North Block of Rum was broadly consistent with observations from culled populations in Norway and Spain, which had much larger sample sizes (Loe *et al.* 2003; Carranza *et al.* 2004). The increase in first molar height from ages 1 to 3 observed in red deer on Rum (Fig. 3) was also observed in the Norwegian red deer study (Loe *et al.* 2003). In this and the Norwegian study, M_1 was measured as the height of the molar perpendicular to the jaw. Changes in the inclination of the tooth relative to the jaw in the first few years of life seem the most likely explanation for this early increase in molar height (Loe *et al.* 2003).

Previous studies of wild red deer populations found faster molar wear in males than females in contrast to the present analyses where no difference between the sexes was found (Loe *et al.* 2003; Carranza *et al.* 2004). The former studies utilized data collected from culled animals, while the present study used natural mortalities. The difference in sampling method may be responsible for the disparity as these sampling methods potentially suffer from different kinds of sampling bias. In both cases, the measures obtained might not represent a random sample of individuals in a given age class. Hunters may select for larger animals or those with the most impressive antlers (Martinez *et al.* 2005) while, conversely, natural winter mortalities may represent the smallest or poorest condition individuals of their age class. Additionally, sampling across ages may not be random. Young or prime-aged individuals may be preferentially culled (Mysterud, Tryjanowski and Panek 2006), while the age distribution of natural deaths will be dictated by the population's age-specific mortality pattern. In the Rum deer, as in many ungulates, this was characterized by heavy mortality in neonates and juveniles followed by low mortality through adulthood and increasing mortality in old age (Fig. 2; Gaillard, Festa-Bianchet and Yoccoz 1998).

The cross-sectional nature of data collected post-mortem means we cannot explicitly account for these potential sources of bias in our analyses (Mysterud *et al.* 2001). However, the fact that additional measures of size at birth and data on survival for the entire North Block study population were also available meant that we were able to test for associations between body size, M_1 and longevity. There was no suggestion that our sample suffered from this potential bias. However, the age structure of our sample was clearly skewed towards young and old individuals. If differences in molar

heights are most evident between the ages of 3 and 9 years, for which sample sizes in the present study were small, then we may have had low power to detect these differences between the sexes. Our sample had notably more data available for individuals aged 10 years or more than either of the previous cull-based studies, which might lead us to expect that if rates of molar wear were faster in males through prime age we should see reduced M_1 among old males relative to females. This did not appear to be the case (Fig. 4). Given the decelerating rate of molar wear documented here and in other studies, both sexes may have reached a lower threshold beyond which M_1 decreases little with age by the time they reach 10 years. Thus, the low sample size of prime-aged individuals in the present study could explain the lack of a difference between the sexes in molar wear rates. However, it is worth noting also that females in the North Block study population experience unusually high population densities that may be associated with increased rates of molar wear. Males typically spend much of their adult life outside the heavily grazed study area, and this ecological difference could also potentially explain the similarity between the sexes.

ECOLOGICAL CORRELATES OF MOLAR HEIGHT AND WEAR

Among females, there were significant differences between population subdivisions in the rate of molar wear with age (Fig. 5A). The lack of variation in longevity between females from different subdivisions means that variation in the effects of tooth wear on survival probabilities associated with different ecological conditions are unlikely to be responsible for these differences. Previous analysis of the study area and population has revealed differences between population subdivisions in both availability of highest quality grazing and the intensity of local resource competition (Clutton-Brock *et al.* 1982; Coulson *et al.* 1997). This local ecological variation could be responsible for the apparent spatial variation in molar wear rates, although genetic or environmental variation in tooth development or eruption cannot be excluded as a mechanism (Kierdorf and Becher 1997).

The rate of first molar decline with age was fastest in females from UG (Fig. 5A). This could be explained by the extremely limited availability of good quality grazing in the southern part of the North Block: females in UG may be forced to consume large quantities of rough, low-quality vegetation and therefore suffer increased rates of tooth wear (Kojola *et al.* 1998). SI females showed the slowest decline in M_1 with age, suggesting that this subdivision represented the least wearing grazing habitat. Average LPDs experienced by females in SI are significantly lower than in LG (SI: 40.3 ± 1.2 SE; LG: 55.1 ± 1.0 SE, $t = 6.70$, $P < 0.001$) or INT (46.8 ± 1.1 SE, $t = 2.84$, $P < 0.01$). LG contains more herb-rich *Agrostis-Festuca* grassland than SI, although SI does contain numerous patches of these

high-quality greens (Fig. 1A). If increased ingestion of soil associated with feeding on heavily grazed, high-quality vegetation is a significant contributor to molar wear (Skogland 1988), then grazing the very heavily used greens in LG may in fact result in increased levels of molar wear relative to more moderately grazed areas.

The paucity of herb-rich greens in INT makes the similarity of molar wear rates between females from this subdivision and LG surprising. We suggest two possible ecological explanations for this. First, females whose home range centroids were in INT showed by far the lowest fidelity to their allocated subdivision. It may be that these deer actually utilize good greens in neighbouring subdivisions and therefore have lower rates of molar wear than would be expected from the area of high-quality grazing present within INT. Second, the small areas of good greens within INT are the only ones fertilized by local gull colonies (Iason *et al.* 1986) and use of the unusually nitrogen-rich vegetation in these areas may be associated with lower molar wear. Planned further and more detailed analysis of both vegetation quality and habitat use in the North Block may help clarify the mechanisms responsible for these spatial differences in molar wear rates.

Females experiencing the lowest LPDs had the least worn M_1 , although this was only true in the two subdivisions with the lowest average LPD (SI and UG) and not in LG or INT (Fig. 5B). The results may simply reflect the fact that only 1% of females from INT or LG experience local densities below 35 individuals, while 47% of females from UG or SI live below this level of resource competition (Fig. 5B). Low LPDs are generally associated with females living in the poorest quality habitats (Coulson *et al.* 1997). However, it may be that at very low levels of local resource competition females can graze more selectively, and ingest either less soil matter or rough plant material. Females in LG and INT may not have experienced low enough local resource competition to reveal an effect on molar height.

EFFECTS OF M_1 WEAR ON FEMALE LATE LIFE FITNESS

There was no evidence that the ability of female deer to provision their last offspring was affected by the degree of wear to their first molar. First molar height is a widely used indicator of molar wear in ungulates (Morris 1972; Aitken 1975). To our knowledge, this study represents the first to test for relationships between molar wear and late-life reproductive success in a wild ungulate population (although see von Hardenberg *et al.* 2003 for a test using incisor morphology and King *et al.* 2005 for an example in wild primates). Although the evidence in this study suggests that among old females those with heavily worn molars can still effectively masticate and digest enough food to reproduce successfully, alternative explanations for the lack of a relationship could not be excluded and should therefore also be considered.

Terminal investment by females in final offspring could result in increased molar wear in the last year of life associated with an increase in energy demand and increased calf birth weights and survival probabilities. This would actually predict a positive relationship between late-life reproduction and molar wear, which was not evident. However, it is possible that terminal investment may mask some detrimental consequences of molar wear in late life. Alternatively, negative consequences of reduced first molar height may be offset by wear revealing compensatory molar surfaces for shearing or grinding food (e.g. King *et al.* 2005). While vertical molar height is reduced over life in deer, molar surface area changes little and the effects of M_1 on digestive efficiency may be limited.

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