Research

The ecology and evolution of tooth wear in red deer and moose

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Differences in body size and diet type (browser–grazer continuum) have formed functional traits of ruminants, including tooth design. Grazers and mixed-feeders eat a more fibrous diet than browsers, which arguably increase tooth wear. Tooth wear has also been suggested to increase with body size. Moreover, for species with large distribution ranges, different populations may be exposed to very different ecological factors affecting diet and thus tooth wear rates. Therefore, evolutionary history and contemporary ecological conditions, both operating through diet, may be important for patterns of tooth wear. Here, we compare inter- and intraspecific rates of tooth wear in multiple populations of one large browser (moose *Alces alces*) and one mixed-feeder (red deer *Cervus elaphus*) covering the main distribution range of each species in Norway. We found that the mixed-feeding red deer wore teeth faster than the larger and browsing moose, suggesting that feeding-type was more important than body size for patterns of wear. There was substantial spatial variation in tooth wear rates, but the inter-specific difference in wear was consistent. Molar wear rates, but not incisors wear rates, in the browser were less variable between populations than in the mixed-feeder. There was no close link between incisor and molar wear rates at the population level. Our findings are consistent with the view that both evolution related to diet type and current ecological conditions (being proxies for within-species variation in diet quality) are important for patterns of tooth wear.

The evolution of permanent dentition was a major event in the early history of mammalian herbivores. Teeth diversified across species to meet functional needs related to efficient mastication and fractioning of different forage items (Evans et al. 2007). Permanent teeth facilitates precise occlusion and thus functionality (Janis and Fortelius 1988), but hold the disadvantage of being gradually and irreversibly worn down. Evolutionary processes act to minimize fitness costs of single traits. Individuals are therefore expected to invest in teeth that last for the expected reproductive lifespan, but not longer (Fortelius 1985, Carranza et al. 2004, Veiberg et al. 2007).

Interspecifically, ungulate foraging ecology and diet are shaped mainly by body mass (Demment and Van Soest 1985) and classified along the browser-grazer continuum (also termed feeding-types, Hofmann 1989). A number of systematic differences along the

gastrointestinal tract function to optimize intake and utilization of a given diet. These adaptations include traits related to forage ingestion (incisor breadth, Gordon and Illius 1988, Perez-Barberia and Gordon 2001), rumino-reticulum processes (Lechner-Doll et al. 1991, Clauss and Lechner-Doll 2001), and post-ruminal energy absorption (Gordon and Illius 1994). The adaptation to different forage along the browser-grazer continuum also includes teeth. Grazers and mixed-feeders feed on a more fibrous diet than browsers (Perez-Barberia et al. 2004). This variation in forage abrasiveness and need for masticatory degradation has caused alteration in both occlusal design (Archer and Sanson 2002), as well as higher molar volume to body mass ratios (equivalent to increased wear resistance) for grazers and mixed-feeders versus browsers (Janis 1988).

Despite the central role of mastication for digestion processes (Perez-Barberia and Gordon 1998), few

studies have compared variation in tooth wear rates between feeding-types (Solounias et al. 1994, Fortelius and Solounias 2000). Molar wear, assessed from hypsodonty indices, was faster in grazers and mixed-feeders than in browsers. The pattern of mesowear, being based on facet development on the occlusal surfaces of the teeth, was also remarkably consistent within, but not among feeding types, both among extant and extinct species. This provides further evidence that feeding types differ in wear rates (Fortelius and Solounias 2000). The role of body mass for tooth wear is uncertain, and theoretical arguments even contest that it should play a role (Fortelius 1987). Solounias et al. (1994) included also body mass in the analysis, but sample size was small (n=7) including only one browser species, the roe deer, *Capreolus capreolus*. The roe deer was also the smallest species in this study (Solounias et al. 1994). Since tooth wear rate correlated positively with body mass, it remains unclear whether the slower wear rate of the browser was actually due to the effect of feeding-type or body mass. Data from a large browser would be enlightening to determine whether feeding-type or body size is the more important for tooth wear rates.

In addition to the above processes, operating mainly on an evolutionary time scale, prevailing ecological conditions may also have considerable impact on tooth wear rates in a given species (Skogland 1988, Kojola et al. 1998, Loison et al. 2001, Nussey et al. 2007). Both population density and habitat quality are predicted to affect dietary quality, which in turn may affect tooth wear. Few studies have presented extensive data on within-species variation in tooth wear, and no study has addressed both the importance of intraspecific, ecological variation and the interspecific, evolutionary background (feeding-type and body size) for patterns of tooth wear. Such a comparison requires extensive data per species and data spanning a wide range of ecological conditions.

Here, we compare tooth wear in multiple populations of one large browser (six populations of moose, *Alces alces*, n=1063) and one mixed-feeder (four populations of red deer, *Cervus elaphus*, n=5519) covering the main distribution range of each species in Norway. If feeding-type is the more important determinant of diet and subsequent tooth wear, we predict H_{1A}: faster overall molar wear in the mixed-feeder compared to the browser (Solounias et al. 1994). However, since the selective feeding strategy of browsers may be associated with more extensive clipping of forage items (i.e. a higher biting rate and less chewing), we predict H_{1B}: that the browser wear incisors faster (absolutely or relatively to molars) than the mixed-feeder. If body size is the most important factor (Solounias et al. 1994), we predict H_2: the larger moose to wear teeth faster than red deer. If ecological conditions are more important for wear rates than the

evolutionary ones (H_{1-2}), we predict H_3: that variation in tooth wear between populations is larger than the variation between species. We also test whether spatial variation in wear can be related to coarse scale population density (cf. Nussey et al. 2007 for the effect of small scale variation in population density), and also whether this potential density dependent relationship is similar in both sexes.

Material and methods

Study area

Both red deer and moose are widely distributed in Norway, but have their main distribution in disparate regions. The red deer data derive from 42 municipalities located in four different regions, covering a north-south gradient along the western coast of Norway (Fig. 1). This includes variation in habitat quality as well as population densities ranging from moderate to high (Mysterud et al. 2001). The main vegetation characteristics of the sampled municipalities fall into the boreone-moral classification with only few local exceptions (Abrahamsen et al. 1977). For study areas in Rogaland/Hordaland (termed population "P1", n = 18 munici-palities), Sogn og Fjordane (termed population "P2",
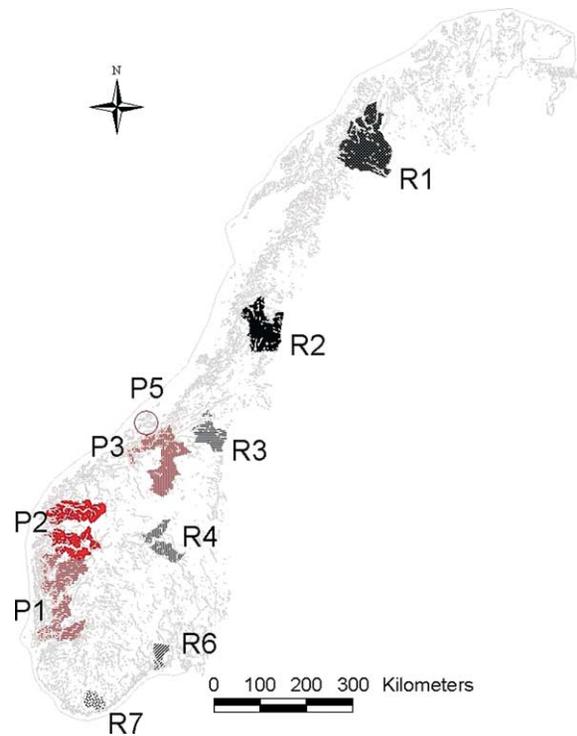

Fig. 1. The spatial distribution of the sampled red deer (termed P1–P3, P5) and moose populations (termed R1–R4, R6 and R7) in Norway.

n = 12 municipalities) and the southern parts of Møre og Romsdal/Sør-Trøndelag (termed population "P3", n = 11 municipalities) the natural forests are dominated by deciduous trees and Scots pine, *Pinus sylvestris*. As a consequence of a large scale programme for planting of Norway spruce, *Picea abies*, initiated in the 1950–1960s, large areas are today covered by dense spruce forest established for commercial timber production (Mysterud et al. 2002). The northern municipalities of P3 are dominated by birch, *Betula pubescens*, and Scots pine. The island municipality of Hitra was treated as a separate population ("P5"). The island is dominated by juniper, *Juniperus communis*, sweet gale, *Myrica gale*, and Scots pine. In general, temperature and precipitation decline from south to north and from coast to inland, while snow depth and number of days with snow cover increase (Langvatn et al. 1996, Mysterud et al. 2000). In summer both the length of the growing season and total degree days decline from southwest to northeast and with increasing altitude.

The moose data derive from 35 municipalities located in six different regions of Norway also covering a north-south gradient (Fig. 1). This spans a very large range of habitat quality and a considerable variation in population density. All regions are situated within the boreal vegetation zone, except for the southernmost region (R7) that also include a part of the nemoral vegetation zone (Moen et al. 1999). Study areas in the counties of Nordland (R2, n = 3 municipalities) and Nord-Trøndelag (R3, n = 5 municipalities) are mainly located in coniferous forests of Scots pine and Norway spruce. In the counties of Troms (R1, n = 9 municipalities) and Oppland (R4, n = 4 municipalities) much of the area is covered by birch in addition to Scots pine and Norway spruce (Oppland only). Forests in the counties of Vestfold/Buskerud/Telemark (R6, n = 10 municipalities) and Vest-Agder (R7, n = 4 municipalities) mainly consist of Scots pine, Norway spruce and birch in the interior parts and coniferous trees mixed with oak, *Quercus robur*, and elements of beech, *Fagus sylvatica*, along the coast. Regional characteristics are further described in detail by Hjeljord and Histøl (1999) and Solberg et al. (2002). We define moose from different regions to belong to different populations (R1–R7; Herfindal et al. 2006). There is considerable spatial variation in primary productivity. Going from coast to inland, from low to high altitude, and from south to north, the length of the winter increase and the length of the growing season decrease (Solberg et al. 2006). In the four southernmost populations, the average growing season (days with average temperature $\geq 5^\circ C$) range between 150 and 210 days, whereas winter temperatures (average for January) range between $0^\circ C$ and $-10^\circ C$, depending on altitude and distance from the coast. Because of the close proximity to the sea, winters can be relatively mild

(average temperature for January between $-6^\circ C$ and $-10^\circ C$) and the growing season relatively long (130–180 days) also in the three northernmost regions.

These spatial variations in habitat likely cause spatial variation in diet, but direct information on diet are not available from all regions. For Norway in general, different browse species dominate moose summer diet (either birch, *Betula* spp., rowan, *Sorbus aucuparia*, willow, *Salix* spp., bilberry, *Vaccinium myrtillus*, or large forbs, Hjeljord and Histøl 1999), while the winter diet also includes spatially various amounts of coniferous twigs (pine, *Pinus sylvestris*). In general, red deer in Norway is a typical mixed-feeder, switching from a mainly herbacious diet during summer (Albon and Langvatn 1992) to more woody forages such as bilberry during winter (Ahlén 1965). Habitat variation was more important than seasonal variation for red deer diet in continental Europe (Gebert and Verheyden-Tixier 2001), so spatial variation in diet and wear can be predicted.

Moose and red deer data

Data are from harvested animals collected as part of the National Monitoring Program for Cervids in Norway. The red deer data consisted of 3002 females (3–25 years) and 2517 males (3–19 years, Table A1). Apart from the material used in Loe et al. (2003) (from years 1971–1975, 1978, 1981, 1983, 1986, 2001), additional material sampled in 2002–2004 was included in the analyses. The moose data originate from animals shot during the regular hunting season, and consisted of 915 females (3–22 years) and 148 males sampled from 2001 to 2004 (3–13 years, Table A1). The underrepresentation of males in the data material is due to the female biased focus of the moose monitoring program and to some extent to a skewed population sex ratio (Solberg et al. 2006). Hunters provided jawbone and they report date and location of harvest, sex and body mass of each culled individual. All animals included were three years or older, which is the age where all individuals have developed the full set of permanent teeth. Age was determined using annuli in the cementum of the first incisor (Reimers and Nordby 1968, Haagenrud 1978, Hamlin et al. 2000). Body mass is dressed weights, i.e. live weight minus head, skin, viscera, bleedable blood and metapodiales (Langvatn 1977), and known to be highly correlated with total body mass (Wallin et al. 1996). Jawbone length (as an index of structural body size) could be measured only for red deer.

Height of the first molar (M_1) was measured as the perpendicular (relative to the jawbone) distance from the peak of the distobuccal cusp to the enamel/cementum line by using a digital calliper (Loe et al.

2003). Equivalently, height of the second incisor (I_2; since I_1 were removed earlier and used for age determination) was measured as the height from the tooth crown to the lower enamel boundary at the anterior middle of the tooth. All measures were recorded with a precision of 0.01 mm.

The hunting season for all the red deer and moose populations is between 10 September and 15 November, though locally there are further restrictions within this time period. The hunting quota system regulating the harvest is quite similar for both species. In general quotas are divided in males, females and calves with the proportion of each category varying with management aims. Local management plans may define additional goals regarding harvest of male and female yearlings.

Local deer density indices

For red deer, we used the total number of animals annually harvested divided by the "qualifying area" in each municipality as an index of population density. The "qualifying area" represent the basis for determining harvest quotas by the local management authorities, and is defined as the area of suitable and available red deer habitat registered within each municipality (Mysterud et al. 2001). This index has proven to correlate well with other indices of population size (Mysterud et al. 2007). Using the same index, we have earlier reported density dependence in body mass (Mysterud et al. 2001) and age of first reproduction (Langvatn et al. 2004). Thus, any lack of density dependence in wear rate is likely to reflect biology rather than the limitations of this index. But, do note that this index pools spatial and temporal variation in density, so it is an index not taking habitat quality and thus resource levels into account.

Moose
Also for moose, we used the number of harvested animals divided by the "qualifying area" in each municipality, i.e. what can be regarded as suitable habitat (Solberg et al. 2006), as an index of density. In addition, we used a combination of harvest data and hunter observations of moose to estimate the winter population density, based on the rational that the annual harvest rate equals the annual recruitment rate when simultaneously controlling for variation in natural mortality rate and population growth rate (Solberg et al. 2006). The winter density, W, was calculated in accordance with the equation:

$$W = \frac{Q \Big/ \left(\left[\frac{R\text{-}M}{1\text{-}R} \right] - \Delta \right)}{A}$$

where Q is the annual harvest of moose in the municipality, R is the proportion of calves seen by hunters during the hunting season (i.e. recruitment rate), M is the natural winter mortality rate in areas without large carnivores (estimated to approximately 5%, Solberg et al. 2005), Δ is the finite annual growth rate, and A is the total municipal "qualifying area". The finite annual growth rate, Δ, was included in the equation to account for the fact that some populations increased or decreased during the study period (1995−2004), indicating that the annual mortality rate (harvest + natural mortality rate) was not balancing the recruitment rate. We estimated Δ as the rate of population change based on the slope, β, of the regression of (ln) seen moose per hunter-day (eight hours) on year during the period 1995−2004 ($\Delta = e^{\beta}-1$). Also Q and R was averaged for the 10 year period 1995−2004 to reduce effects of random variation in hunting success or animal detectability between years.

The average winter density of moose for the period 1995−2004 varied extensively between municipalities (range: 0.19−2.58) and correlated positively with the moose density index calculated as moose killed per unit qualifying area (r = 0.845 [0.828, 0.862]).

Statistical analyses

We know from earlier studies that tooth wear rates differ between males and females in moose (Ericsson and Wallin 2001) and red deer (Loe et al. 2003, Carranza et al. 2004). Moreover, life history traits differ largely among sexes in polygynous, sexually dimorphic ungulates. We therefore ran separate analyses for males and females in both species.

All tooth height measures were log-transformed (ln). To test the evolutionary predictions (H_{1-2}), we first fitted two linear models (LM's), the first model with (ln) height of M_1 and the second with (ln) height of I_2 as response variable. Both models included species, age (continuous in years) and the interaction as predictor variables. A significant interaction between species and age in the two models would imply different interspecific wear rates for molars and incisors respectively. To investigate the interspecific difference in wear rates between molars and incisors (H_{1B}) we compared the ratio of the two incisor slopes with the ratio of the two molar slopes. The two ratios tell how much faster red deer wear respectively incisors and molars compared to moose.

To quantify interspecific (between species) vs intraspecific (between population) variation in tooth wear, we fitted two linear mixed-effects (LME) models, the first using (ln) height of M_1 and the second with (ln) height of I_2 as response variable. Both models

included age as fixed effect and population nested within species as random slopes, and included only females due to the low number of male moose. We used restricted maximum likelihood (REML) estimation because it provides the most reliable estimates of the variance components (Venables and Ripley 1999). We assessed the standard deviation (SD) with associated 95% confidence limits (CI) for each of the random slopes. To compare between-population variation we fitted LME's separately for the two species, using (ln) M_1 or (ln) I_2 as response variables, age as fixed effect and population as random slope.

Due to non-overlapping study areas of moose and red deer, analyses of spatial variation (H_3) in tooth wear rates were done separately for the two species and for each sex. In these analyses we also used (ln) height of M_1 and (ln) height of I_2 as response variables. All biologically relevant variables of expected relevance to tooth height, as well as selected two-way interactions, were included as predictors in the model. The predictor variables were: 1) population (regions in Norway), 2) body size (jaw length in red deer and body mass in moose), 3) local (municipal) deer density, 4) age, and the interactions 5) age × density, 6) age × body size, and 7) age × population. Interaction 5) identifies density dependence in tooth wear, and interaction 7)

describes population differences in tooth wear rate. A negative parameter estimate of the interactions implies a faster wear rate, while a positive estimate implies a slower wear rate, compared to lower densities or a reference population respectively. All continuous variables were standardised to facilitate direct comparison. Two-way interactions between continuous variables were fitted as the multiplicative term of the two standardised variables (Portier et al. 1998).

For each species, sex and tooth type, we used AIC to select the best models, starting with the full model described above (Burnham and Anderson 2002). The stepAIC function in the R library MASS was used to find the best models. As a check, these findings were subsequently compared with the results from manual fitting of a series of candidate models. Finally, we fitted a LM including all parameters selected in the best model and presented their parameter estimates with associated 95% confidence limits (CI; Table 1 and 2). A parameter is considered significant when the 95% CI does not overlap zero.

The number of animals in each age class declined with increasing age (Table S1). In the electronic appendix we therefore present alternative models when the oldest individuals are removed, to investigate if the results from the full models depend on a few old

Table 1. Two models describing the relationship between molar tooth height (M_1) and various predictor variables in female and male red deer. The two presented models were our most complex candidate models which performed better than all simpler candidate models according to the AIC criterion. All continuous variables are standardised to facilitate direct comparison and two-way interactions between continuous variables are fitted as the multiplicative term of the two standardised variables. The reference level for the population effect is population P1.

	Parameter estimate	SE	95% CI
Female red deer			
Intercept	2.27	0.00456	2.26, 2.28
Population (P2−P1)	0.0326	0.00574	0.0218, 0.0439
Population (P3−P1)	0.0309	0.00645	0.0183, 0.0436
Population (P5−P1)	−0.0163	0.00874	−0.0334, 0.000820
Jaw length	0.0223	0.00253	0.0173, 0.0272
Density	−0.0172	0.00245	−0.0220, −0.0124
Age	−0.176	0.00482	−0.185, −0.166
Age × density	0.00383	0.00254	−0.00115, 0.00881
Age × jaw length	0.00899	0.00231	0.00446, 0.0135
Age × population (P2−P1)	0.00471	0.00578	−0.00662, 0.0160
Age × population (P3−P1)	0.0101	0.00675	−0.00310, 0.0234
Age × population (P5−P1)	−0.0378	0.00836	−0.0542, −0.0214
Male red deer			
Intercept	2.41	0.00381	2.40, 2.42
Population (P2−P1)	0.0347	0.00504	0.0249, 0.0446
Population (P3−P1)	0.0294	0.00539	0.0188, 0.0399
Population (P5−P1)	0.00766	0.00692	−0.00590, 0.0212
Jaw length	0.0280	0.00217	0.0238, 0.0323
Density	−0.0216	0.00226	−0.0260, −0.0171
Age	−0.0931	0.00389	−0.101, −0.0855
Age × density	−0.00491	0.00222	−0.00926, −0.000562
Age × jaw length	−0.00578	0.00186	−0.00943, −0.00213
Age × population (P2−P1)	−0.00800	0.00518	−0.0181, 0.00215
Age × population (P3−P1)	0.0185	0.00553	0.00772, 0.0294
Age × population (P5−P1)	−0.0209	0.00614	−0.0329, −0.00885

Table 2. The best models (according to the AIC criterion) describing the relationship between molar tooth height (M_1) and various predictor variables in female and male moose. Male moose data are very scarce (Fig. 3d) and the only factor entering the model is age. All continuous variables are standardised to facilitate direct comparison. Two-way interactions between continuous variables are fitted as the multiplicative term of the two standardised variables. The reference level for the population effect is population Troms, R1.

	Parameter estimate	SE	95% CI
Female moose			
Intercept	2.59	0.00831	2.57, 2.60
Age	−0.101	0.00817	−0.117, −0.0851
Population (R2−R1)	0.0334	0.0128	0.00836, 0.0585
Population (R3−R1)	0.0532	0.0119	0.0298, 0.0766
Population (R4−R1)	0.0823	0.0112	0.0603, 0.104
Population (R6−R1)	0.0568	0.0105	0.0363, 0.0772
Population (R7−R1)	0.0619	0.0111	0.0401, 0.0837
ln (body mass)	0.00643	0.00338	−0.000204, 0.0131
Age × ln (body mass)	0.00505	0.00334	−0.00151, 0.0116
Age × population (R2−R1)	0.0258	0.0127	0.000866, 0.0507
Age × population (R3−R1)	0.00502	0.0117	−0.0180, 0.0280
Age × population (R4−R1)	0.0196	0.0111	−0.00225, 0.0414
Age × population (R6−R1)	0.00232	0.0107	−0.0186, 0.0233
Age × population (R7−R1)	0.0298	0.0111	0.00812, 0.0515
Male moose			
Intercept	2.70	0.00666	2.69, 2.71
Age	−0.0415	0.00668	−0.0546, −0.0284

individuals. To correct for imbalances in the data material from different populations, we carried out repetitive model selections as the oldest age classes were gradually excluded (independent of which population they belonged to). The age cut-off point was selected to ensure balance in the representation of age classes among populations; therefore the number and percentage of outliers removed differ among species and sexes (Table A2, A3).

Finally, we checked if the choice of density indices and body size measures affected parameter estimates in the models. For moose, we replaced the preferred density index with "number of animals harvested per km^2 of suitable habitat" (the density index used for red deer). In red deer, we also ran the models using body mass instead of jaw length as a measure of size (as done for moose). The new models contained no qualitative changes, suggesting that the results were robust.

All statistical analyses were conducted using the statistical software R ver. 2.4.1, R Development Core Team 2006. We used the library nlme when fitting LME's.

Results

Consistent with H_{1A}, but opposite to H_2, the smaller, mixed-feeding red deer wore molars 2.0 times faster (ratio between slopes; Fig. 2a) and incisors 2.3 times faster (Fig. 2b) than the browsing moose (parameter estimates for the feeding-type × age interaction; molars:

estimate = −0.0201 [−0.0220, −0.0182]; incisors: estimate = −0.0170 [−0.0191, −0.0148]). Slope estimates for tooth wear in all red deer populations were consistently steeper than in all moose populations for both molars (Fig. 3) and incisors (Fig. 4), indicating the opposite of prediction H_{1B} (faster incisor wear in moose).

Both male and female red deer showed pronounced differences in molar (Fig. 3a−b) and incisor (Fig. 4a−b) wear rates between populations; even after accounting for differences in local density (Table 1 and 3). While interspecific and intraspecific incisor wear were of similar magnitude ($SD_{species} = 0.0164$ [0.00358, 0.0755]; $SD_{populations} = 0.0105$ [0.00646, 0.0172]; including females only), between species variability in molar wear was higher than the variability between populations ($SD_{species} = 0.0143$ [0.00349, 0.0587]; $SD_{populations} = 0.00350$ [0.00204, 0.00600]; including females only). H_3, predicting larger interspecific than intraspecific variability in tooth wear rates, was therefore only supported when using molars. Across populations, there was no close match between molar and incisor wear rates (Fig. 3 vs Fig. 4). While female and male red deer in P5 wore molars more rapidly than other populations, they did not differ from most other populations in rate of incisor wear (Fig. 3a−b vs Fig. 4a−b; Table 1 vs Table 3). Red deer males in the region P3 wore molars slower than in other regions, but they wore incisors more rapidly (Table 1 and 3). When the oldest females were excluded from the dataset, females from P2 and P3 were found to have significantly
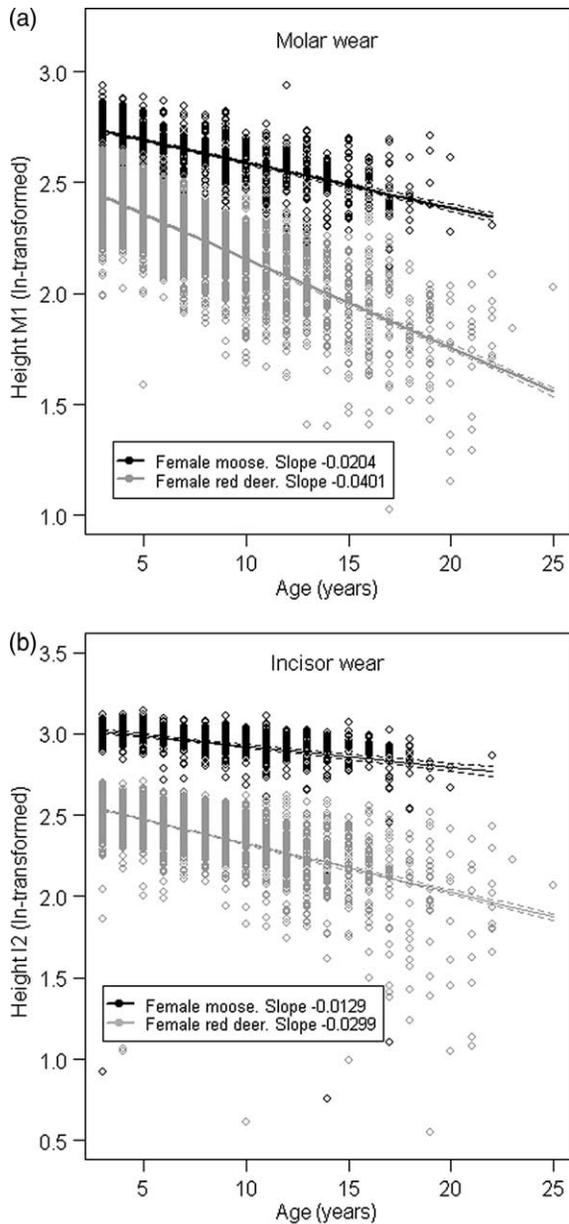
Fig. 2. The relationship between age and height of the a) first molar (M_1) and b) the second incisor (I_2; both ln-transformed) in female moose (black) and red deer (grey). Solid lines represent predicted values for every population. Dotted lines give the 95% confidence limits.

slower molar wear rates than the reference population (Table A2). Excluding the oldest females did not alter population wear rates of incisors (Table A4). Removal of the oldest males caused no qualitative alteration of the age × population interaction for molars (Table A2) or incisors (Table A4).

Female moose showed less variation in tooth wear rates among populations ($SD_{molars} = 0.00247$

[0.00103, 0.00595]; $SD_{incisors} = 0.00352$ [0.00153, 0.00806]) than female red deer ($SD_{molars} = 0.00504$ [0.00234, 0.0108]; $SD_{incisors} = 0.00959$ [0.00440, 0.0209]). Still, populations of female moose wore molars and incisors at significantly different rates (Fig. 3c, 4c; data from male moose are too limited to conclude, Fig. 3d, 4d). Also for moose, there was no close match between incisor and molar wear at the population level (Fig. 3c vs Fig. 4c; Table 2 vs Table 4). Females in the populations R2 and R7 wore molars slower than the reference population (R1; see parameter estimates of the age × population interaction in Table 2), while R3 was the only population that wore incisors faster than the reference population (Table 4). Exclusion of the oldest individuals caused the age × body mass interaction to drop out of the best model for molars (Table A3). In addition, the difference in molar wear rates between populations R2 and R1 turned non-significant and density entered the best model (indicating overall smaller molars at high densities; Table A3). When excluding the oldest individuals in the incisor model, females in population R7 wore incisors significantly faster than in the reference population (Table A4). Due to limited sample size, the model for male moose was very unstable (interactions in and out), and the age effect on wear was the only robust result (Table A4). Note also that the interaction between age and body size that entered some models, was not consistent in direction and depended on inclusion of a few very old animals (details in Appendix 1).

Male red deer wore both molars and incisors more rapidly at increasing population densities (a negative interaction for age × density when controlling for other factors; Table 1). In females a similar effect was found for incisor wear only (Table 2); however this effect was depending on including the oldest individuals in the model (Table A4). For molars, there was in fact a tendency for decreasing wear rates at higher densities (Table 1), but also this effect dropped out when excluding old individuals (Table A2). Molar and incisor wear in female moose was not related to population density (the interaction age × density was not included in the best model; Table 2, 4; excluding the oldest individuals had no effect, Table A3, A5).

Maximum tooth height (at three years of age), controlling for individual differences in body size and local deer density, showed modest differences between populations both in red deer and moose (molars: Fig. 3a–c; incisors: Fig. 4a–c). The red deer populations with the fastest molar wear rates had the smallest predicted maximum tooth heights (Fig. 3a–b). For incisors in both species, and for molars in female moose, there appeared to be no relationship between maximum tooth heights and wear rates (Fig. 3c).
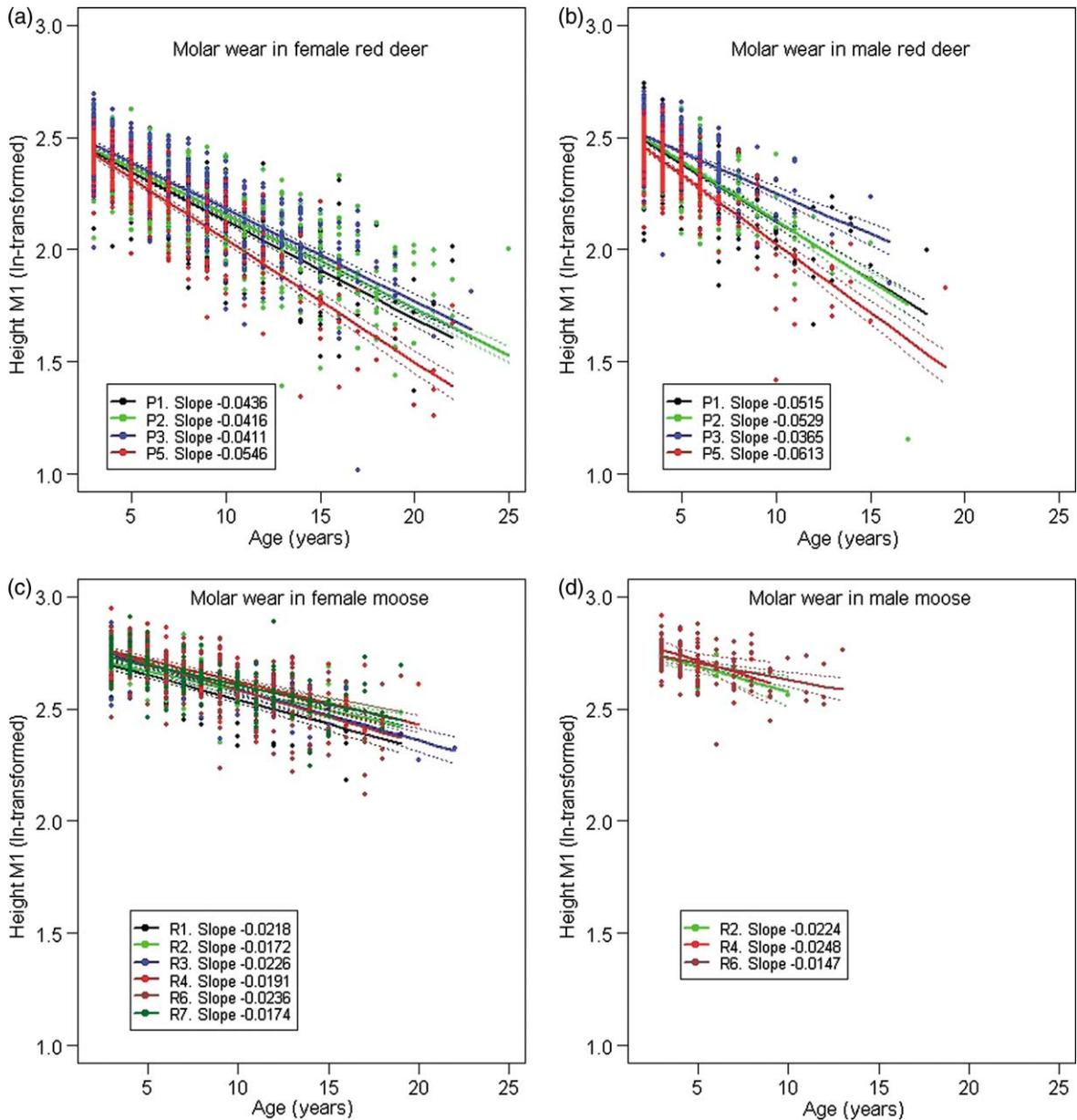
Fig. 3. Population differences in molar (M_1) wear by age in (a) female red deer, (b) male red deer, (c) female moose, and (d) male moose, controlling for differences in local deer density and body size (jaw length in red deer and body mass in moose). Solid lines represent predicted values for every population. Dotted lines give the 95% confidence limits.

Discussion

We found that the mixed-feeding red deer wear teeth faster than the larger and browsing moose, suggesting that feeding-type was more important than body size for patterns of wear. There was substantial spatial variation in tooth wear rates both among red deer and moose populations, but the interspecific difference was larger as slope estimates of wear did not overlap. However, between species variation was larger than between population variation for molars, but not for incisors. Between population variation in molars was also higher for red deer than for moose. There was no close link between incisor and molar wear rates at the population level. Density dependence in wear rates was only consistent in male red deer, indicating that
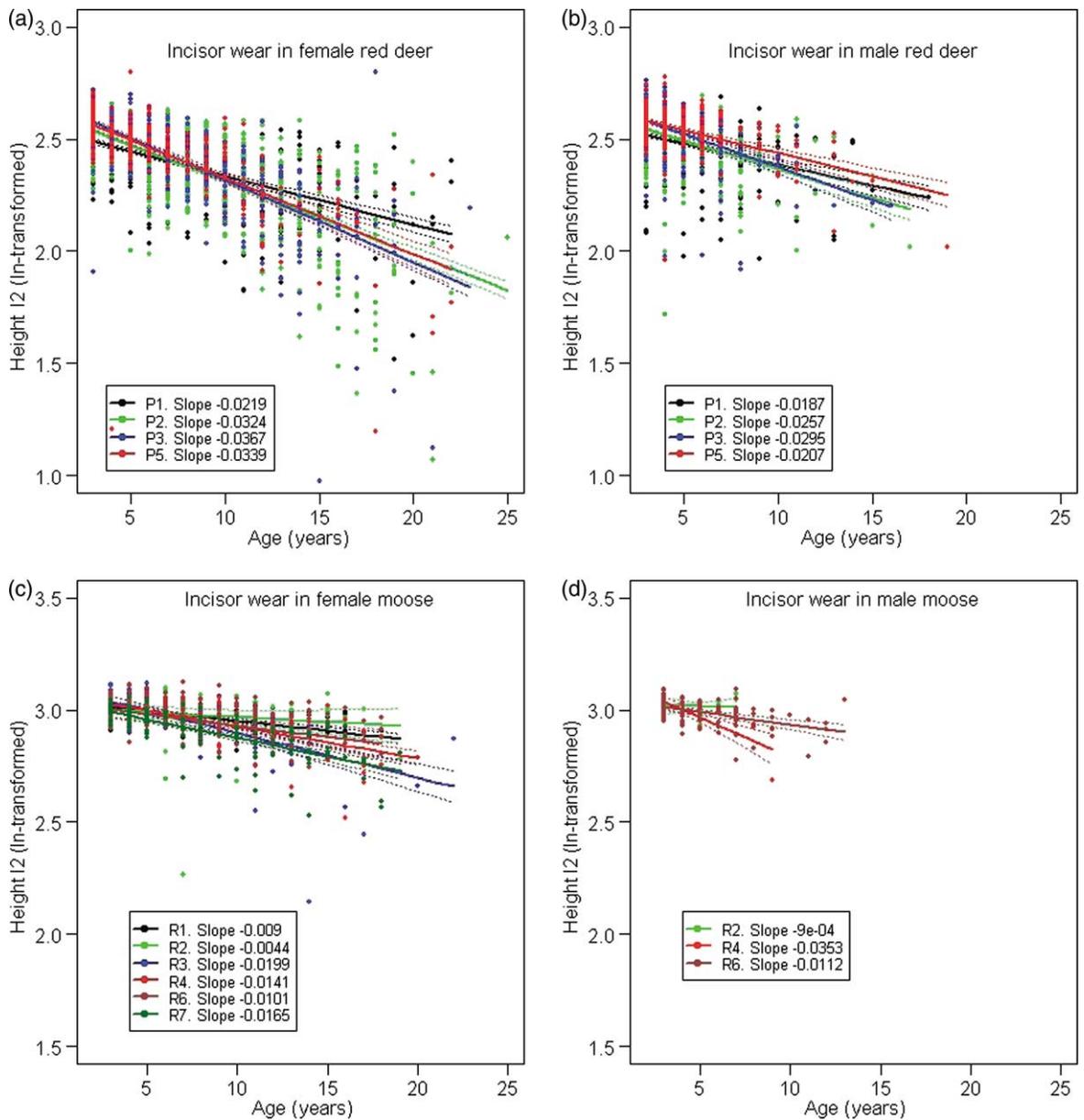
Fig. 4. Incisor (I_2) wear by age in different populations of (a) female red deer, (b) male red deer, (c) female moose, and (d) male moose, controlling for differences in local deer density and body size (jaw length in red deer and body mass in moose). Solid lines are predicted values for each population. Dashed lines give the 95% confidence limits.

environmental variables and habitat quality were more important than density per se for generating spatial variation in tooth wear.

Faster tooth wear in the mixed-feeder than in the browser

The interspecific difference in tooth wear rate is probably caused by feeding-type related differences in forage quality. The fibrous content and the mastication effort per unit of forage is expected to increase from browsers via mixed-feeders to grazers (Van Soest 1994). Regardless of feeding-type, molar volume scale isometrically with body mass (Janis 1988). Differences in molar wear rates across feeding-types will therefore either be linked to variation in forage ingestion rate, forage quality or the accumulation of dust and grit on the food (Janis 1988). Solounias et al. (1994) found that browsers and grazers exhibited a respectively lower

Table 3. The best model for incisor (I_2) wear in female and male red deer. All continuous variables are standardised. Two-way interactions between continuous variables are fitted as the multiplicative term of the two standardised variables. The reference level for the population effect is population P1.

	Parameter estimate	SE	95% CI
Female red deer			
Intercept	2.41	0.00487	2.40, 2.42
Population (P2−P1)	0.0154	0.00610	0.00346, 0.0274
Population (P3−P1)	0.0290	0.00687	0.0156, 0.0425
Population (P5−P1)	0.0415	0.00922	0.0234, 0.0595
Jaw length	0.0105	0.00269	0.00519, 0.0157
Density	−0.00504	0.00261	−0.0101, 0.0000705
Age	−0.0862	0.00511	−0.0962, −0.0762
Age ×density	−0.00550	0.00269	−0.0108, −0.000224
Age ×jaw length	−0.00925	0.00245	−0.0141, −0.00444
Age ×population (P2−P1)	−0.0392	0.00612	−0.0512, −0.0272
Age ×population (P3−P1)	−0.0528	0.00714	−0.0668, −0.0388
Age ×population (P5−P1)	−0.0381	0.00889	−0.0555, −0.0207
Male red deer			
Intercept	2.49	0.00360	2.48, 2.50
Population (P2−P1)	0.0283	0.00483	0.0188, 0.0378
Population (P3−P1)	0.0491	0.00515	0.0390, 0.0592
Population (P5−P1)	0.0792	0.00654	0.066, 0.0920
Jaw length	0.00986	0.00205	0.00583, 0.0139
Density	−0.00647	0.00216	−0.0107, −0.00225
Age	−0.0380	0.00361	−0.0450, −0.0309
Age ×density	−0.00824	0.00208	−0.0123, −0.00416
Age ×population (P2−P1)	−0.0137	0.00493	−0.0234, −0.00405
Age ×population (P3−P1)	−0.0274	0.00522	−0.0377, −0.0172
Age ×population (P5−P1)	0.00803	0.00578	−0.00331, 0.0194

and higher molar wear rate than mixed-feeders as expected from overall dietary fibre content. They only included one browser, the roe deer, which also happened to be the smallest species in their study.

The wear rates reported here for moose, the biggest contemporary browsing cervid, thus provide the first evidence of lower molar wear rates in a browser irrespective of body mass. Further, this increased

Table 4. The best model for incisor (I_2) wear in female and male moose. All continuous variables are standardised. Two-way interactions between continuous variables are fitted as the multiplicative term of the two standardised variables. The reference level for the population effect is population R1. In males, the population differences in wear rate disappear when excluding seven old males in one population (Table S5 in the electronic appendix).

	Parameter estimate	SE	95% CI
Female moose			
Intercept	2.94	0.0148	2.91, 2.97
Population (R2−R1)	−0.00158	0.0180	−0.03697, 0.0338
Population (R3−R1)	0.0160	0.0204	−0.0241, 0.0561
Population (R4−R1)	0.00324	0.0155	−0.0272, 0.0337
Population (R6−R1)	0.0526	0.0246	0.00427, 0.101
Population (R7−R1)	−0.0148	0.0198	−0.0536, 0.0241
Density	−0.0323	0.00925	−0.0504, −0.0141
Age	−0.0393	0.0103	−0.0596, −0.0191
Age ×population (R2−R1)	0.0175	0.0179	−0.0176, 0.0527
Age ×population (R3−R1)	−0.0417	0.0155	−0.0721, −0.0113
Age ×population (R4−R1)	−0.0207	0.0144	−0.0491, 0.00764
Age ×population (R6−R1)	−0.00390	0.0133	−0.0299, 0.0221
Age ×population (R7−R1)	−0.0268	0.0147	−0.0556, 0.00195
Male moose			
Intercept	3.02	0.0131	2.99, 3.04
Population (R4−R2)	−0.0531	0.0180	−0.0886, −0.0175
Population (R6−R2)	−0.0297	0.0142	−0.0578, −0.00159
Age	0.00902	0.0217	−0.0339, 0.0519
Age ×population (R4−R2)	−0.0756	0.0265	−0.128, −0.0232
Age ×population (R6−R2)	−0.0345	0.0223	−0.0786, 0.00948

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chewing investment in mixed-feeders compared to browsers is expected to affect the molars more than the incisors. However, our results show that absolute wear of incisors and molars was 2.3 and 2.0 times faster in red deer than in moose, respectively (Fig. 2). Molar wear rate in both species was, on the other hand, relatively faster than incisor wear rates (red deer: 1.6 and moose: 1.3 times faster). Although molar wear rates varied intraspecifically, the interspecific pattern of the browser wearing molars at a slower rate was consistent across the full range of populations and the molar wear rates were much more variable between species than between populations of the same species. Considering the large distribution range, the two species experience substantial ecological variation. Still, the consistency of species-specific molar wear patterns suggests that sub-sampling within species is a minor source of variation in comparative studies.

Molar vs incisor wear

Former studies of tooth wear were focusing on molars, while we present the first extensive analysis of both molar and incisor wear. Plant material can be functionally divided into cell constituents and cell wall (Van Soest 1994). It is assumed that browsers show selectivity mainly for cell content (and thus avoid grasses), while grazers (and mixed-feeders) have more efficient plant cell wall fermentation (Hofmann 1989). As effective fermentation requires more thorough mastication, one could speculate that molars should be relatively more important for grazers and incisors relatively more important for browsers (H_{1b}). However, we found no evidence of faster incisor wear of the browsing moose compared with the mixed-feeding red deer. For incisors, between-population variation in wear was similar in magnitude to between species variation, in contrast to the pattern for molars. This suggests that current ecological conditions affecting diet are more important for wear rates of incisors than for molars. Unfortunately, there is not enough dietary studies of the two species at the scale of our populations to enable a direct analysis of tooth wear relative to diet quality.

We are the first study to document that there is no close match between molar and incisor wear rates among populations. The molar wear for red deer was clearly fastest in the high density population inhabiting the low quality habitat on the island Hitra ("P5"), but incisor wear was fairly average. We may speculate that ingestion of poor quality food affect incisors and molars differently. Poor quality food requires more mastication by molars (increasing molar wear) and possibly prolonged rumen retention time. This may in turn reduce overall food intake (reducing incisor wear). These issues clearly warrant further studies.

Spatial variation in tooth wear

Our data derive from the whole distribution range of red deer and moose in Norway. Life history variation related to population density and habitat differences among these populations have been reported in both moose (Herfindal et al. 2006) and red deer (Mysterud et al. 2001, 2002). Arguably, the moose data come from a wider range of habitats, but molar wear patterns seem to be less spatially variable. Whether or not this reflects real differences between grazers/mixed-feeders vs. browsers still remain to be determined. Other studies of spatial variation in molar wear derive from mixed-feeders such as reindeer/caribou (Skogland 1988, Kojola et al. 1998, Loison et al. 2001) and red deer/elk (Garrott et al. 2002, Nussey et al. 2007). Limited variation in molar wear between populations of the browsing roe deer (Hewison et al. 1999, Veiberg et al. 2007) may suggest that lower variation in molar wear rates among browser populations is a consistent pattern.

Ungulates may compensate for rapid wear by evolving higher teeth (Fortelius 1985). We found modest differences in maximum molar and incisor height in both sexes of red deer and in female moose. Red deer in populations with the smallest molars tended to wear teeth more rapidly, implying that maximum tooth height may be limited by the same factors that lead to rapid wear. For molars in moose and for incisors in both species, there was no relationship between maximum tooth height (at three years of age) and wear rate, as would be expected if individuals in populations with rapid wear evolve higher teeth. These populations are heavily harvested with a very low life expectancy (Langvatn and Loison 1999). Since most individuals are shot at young age, tooth height is currently not a limiting factor to lifespan and evolution of higher teeth to compensate for high wear rates, is therefore not expected to occur.

Spatial differences in tooth wear − a role for population density?

Density dependence is an important process shaping life histories in ungulates (Fowler 1987, Gaillard et al. 2000). As density increases in a given area, ungulates often eat a lower quality diet (Fowler 1987, Freeland and Choquenot 1990), which may explain a higher rate of tooth wear as well as earlier onset of senescence (Mysterud et al. 2001).

Our density estimates include both temporal and spatial components of density, which may thus reflect a mixture of processes, i.e. "true" density effects and habitat quality. We cannot control for the possibility that better habitat quality is associated with elevated population densities. This problem was most acute for

the moose data that originated from only a few years, which enabled us to only make a spatial contrast in density. In contrast, part of the red deer data originates from the period 1971 to 1975 – before the recent large increase in population density – adding a larger temporal contrast in density. In any case, the spatial contrast in population density was unable to account for all of the spatial variation in tooth wear. This may suggest that population density per se is of less importance compared to spatial variation in habitat quality. If habitat quality is better in areas of high density, this may lead to lower wear rates than expected from density alone, and may explain why we failed to find strong density effects. A different result may have appeared if we had only variation in density for a given population over time, and thus could neglect spatial variation in habitat quality. Nussey et al. (2007) reported density dependent variation in tooth wear rates in red deer females on parts of the island of Rum, Scotland. Further, the spatial scale of the North Block of Rum (within 12 km^2) is smaller than the scale of the municipalities included here (Fig. 1), which may make a difference.

Life history and foraging ecology is sex-dependent in polygynous ungulates, and indeed, for males there was significant density dependence in wear rates, as predicted earlier based on patterns of somatic senescence (Mysterud et al. 2001). Male and female red deer live sexually segregated through most of their lives (Bonenfant et al. 2004) occupying different habitats (Clutton-Brock et al. 1987, Conradt et al. 1999), and accordingly density dependence may affect male and female habitats differently. Clearly, density dependence in molar wear rates is thus not a universal phenomenon, and the causes of this variation remain to be determined.

We base our findings on transversal and not longitudinal data, as is the case for all studies of tooth wear this far. Repeated measures from identified animals over a given period of time would therefore have represented a considerable strengthening of our data set regarding the defined approaches. Attaining such information from wild populations is, on the other hand, extremely time and resource demanding.

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Appendix 1.

(Available online as Appendix O16159 at www.oikos. ekol.lu.se)