Evidence for a trade-off between early growth and tooth wear in Svalbard reindeer

VEBJØRN VEIBERG*†, ATLE MYSTERUD†, EIRIN BJØRKVOLL*‡,
ROLF LANGVATN*, LEIF EGIL LOE†, R. JUSTIN IRVINE§,
CHRISTOPHE BONENFANT†¶, FRED COUWELEERS** and
NILS CHR. STENSETH†

*University Centre in Svalbard, Department of Arctic Biology, PB 156, N-9171 Longyearbyen, Norway; †Centre for Ecological and Evolutionary Synthesis, Department of Biology, University of Oslo, PO Box 1066 Blindern, N-0316 Oslo, Norway; ‡Norwegian University of Science and Technology, Department of Biology, N-7491 Trondheim, Norway; §The Macaulay Institute, Craigiebuckler, Aberdeen AB15 8HQ, Scotland, UK; ¶UMR 5558 'Biométrie et Biologie Evolutive', Université Claude Bernard-Lyon 1, 43, Boulevard du 11 Novembre 1918, 69622 Villeurbanne Cedex, France; and **Department of Optical Measurement Systems and Data Analysis, SINTEF ICT, 7465 Trondheim, Norway*

Summary

1. Ruminants depend on efficient physical degradation of forage through chewing to increase the surface area of the food particles presented to the microflora. Fossil evidence suggests that increased molar height is an adaptation for wear tolerance in dry ecosystems with sparse vegetation, but no study has shown selection pressure for hypsodonty in contemporary ruminants.

2. We explored the relationships between particle size in rumen, tooth wear (scanned molar occlusal topography), age and body mass of female Svalbard reindeer living in an arctic desert at 78° latitude on Svalbard.

3. We predicted that (H1) if the rumen particle size is determined mainly by constraints due to tooth wear, and if tooth wear is mainly a function of age, average particle size in rumen should increase with age. From allometric relations it is known that larger individuals can survive on a lower-quality diet, we therefore predicted (H2) larger particle sizes with increases in (ln) body mass, irrespective of age and wear. Lastly, if there is a trade-off between growth and tooth wear in dry ecosystems (a selection pressure for hypsodonty), we predicted (H3) that teeth of heavier animals should be more worn than those of lighter animals of the same age.

4. The proportion of small particles (<1·0 mm) decreased rapidly with increasing age (consistent with H1). Heavier females within an age class had more worn teeth (consistent with H3) than lighter ones. A close-to-isometric relationship between particle size and body mass suggested that heavier animals partly compensated for reduced tooth efficiency by chewing more.

5. We provide the first evidence of a trade-off between fast early growth and wear (a somatic cost) of a senescence-related trait – the structure and height of the molar – in a wild ruminant inhabiting an arctic desert where selection pressure for increased tooth height is expected. This suggests that foraging conditions are more extreme than the environment in which the species originally evolved.

Key-words: foraging ecology, life history, optimal digestion, *Rangifer tarandus platyrhynchus*, ungulate.

Correspondence: Atle Mysterud, Centre for Ecological and Evolutionary Synthesis, Department of Biology, University of Oslo, PO Box 1066 Blindern, N-0316 Oslo, Norway. Tel.: +47 22 85 40 45. Fax: +47 22 85 47 26. E-mail: atle.mysterud@bio.uio.no

Introduction

From a herbivore perspective, the major functional division of plant material is between the cell constituents and the cell wall (Van Soest 1994). Cell contents are the fraction active in plant metabolism and composed primarily of sugars, proteins and storage carbohydrates, which can be digested directly by herbivore enzymes or fermented rapidly by microbes. The cell wall fraction consists mainly of cellulose, hemicellulose and lignin, and is not degraded by most herbivore enzymes. Ruminants are, however, especially adapted to extracting energy from these structural carbohydrates by fermentation through a symbiotic association with anaerobic microbes in their reticulo-rumen. However, fermentation rate is strongly affected by the size of the food particles presented to the microflora, as these microorganisms are themselves inefficient in reducing particle size (Van Soest 1994). Efficient physical degradation of forage through chewing to increase forage surface area is therefore vital to decrease digestion time (Perez-Barberia & Gordon 1998a), which is a major constraint in the time budget of ruminants (Belovsky 1978).

A cornerstone in foraging theory of ruminants is that energy requirements scale allometrically with body mass ($M^{2/3}$; White & Seymour 2003), while rumen volume and gut capacity are isometric with size (Demment & Van Soest 1985). From these relationships, one can derive that smaller ruminants require more energy per kg body mass than larger ones, allowing larger ruminants, both intra- and interspecifically, to survive on a lower-quality diet (Bell 1971; Jarman 1974). Smaller ruminants may acquire this extra energy needed by selecting a diet of higher quality, or alternatively by more thorough mastication than bigger animals if foraging on the same diet (Gross *et al*. 1995). However, increased mastication potentially has its price in terms of increased tooth wear and thus reduced potential for further growth or energy gain. To compensate for a gradual physical deterioration caused by wear, the mastication effort needed to maintain even a constant energy supply will increase. Therefore mastication and subsequent tooth wear represent an unusually direct link between foraging processes and life history. Despite this, data on the relationship between tooth wear and key life-history parameters such as body mass remain surprisingly scarce.

The forage mastication process can be seen as a balance between energy requirements (derived from body size relationships) and tooth wear, which may result in life-history trade-offs or investment patterns. Increased molar height, termed hypsodonty, is an adaptation for wear tolerance. Fossil evidence suggests that hypsodonty in ruminants is linked to dry climate, although it remain uncertain whether the mechanism relates to increased fibrousness and decreased nutritive value, or to increased abrasiveness due to intracellular silica or extraneous dust (Fortelius 1985; Janis 1988; Fortelius *et al*. 2002). No study has shown selection pressure for hypsodonty in contemporary ruminants. Localized at 78–79°N, the Svalbard reindeer (*Rangifer tarandus platyrhynchus* Vrolik) inhabits an extreme arctic desert with a low annual precipitation (≈350 mm) and average temperatures below 10 °C in all 12 months of the year (Hanssen-Bauer, Kristensen Solås & Steffensen 1990). The vegetation coverage is sparse, the tooth wear rate is high (Tyler *et al*. 1986), and occasionally severe die-offs during winter have been reported (Chan *et al*. 2005). In this study, we investigate the relationship between rumen particle size, age, body mass and tooth wear in Svalbard reindeer. As a measure of tooth wear, we use the ruggedness of the grinding teeth as derived from a novel method describing the three-dimensional structure of the occlusal surface of molar teeth extracted from digital photos. Using the proportion of small particles in the rumen as a measure of the efficiency of mastication, and also controlling for variation in diet composition, we test the following hypotheses.

H1: THE TOOTH WEAR-CONSTRAINT HYPOTHESIS

If the rumen particle size is determined mainly by constraints due to tooth wear, and if tooth wear is mainly a function of age (Skogland 1988; Kojola *et al*. 1998; Loe *et al*. 2003; Carranza *et al*. 2004), average particle size in rumen should increase with age. There should be no residual effect of age on rumen particle size after adjusting for tooth wear and body mass.

H2: THE ALLOMETRY, OPTIMALITY HYPOTHESIS

From allometric relations (and an optimality way of thinking), it is known that smaller ruminants require more energy per kg body mass than larger ones, allowing larger ruminants to survive on a lower-quality diet (details above), we therefore predict larger rumen particle sizes with increasing body mass, irrespective of age and tooth wear (Clauss, Lechner-Doll & Streich 2002).

H3: THE GROWTH-INVESTMENT HYPOTHESIS

If there is a trade-off between growth and tooth wear, teeth of heavier animals should be more worn than lighter animals of the same age, and thus suggestive of a selection pressure for hypsodonty.

Materials and methods

STUDY AREA

Data was collected from two areas, Colesdalen/Reindalen (77°57′ N, 15°30′ E) and Sassendalen (78°15′ N, 17°20′ E), in Nordenskiöldland, Spitsbergen, Svalbard. The region is characterized by wide valleys surrounded by steep mountains and glaciers. Minimum distance along valleys connecting the two areas is ≈40 km.

Despite this relatively short distance, a genetic study has shown that little exchange of animals takes place (Côté *et al.* 2002). Helicopter surveys conducted annually during the summers since 1992 indicate that the reindeer population size in both areas is ≈700 (Governor of Svalbard, unpublished data). Hunting pressure is generally low and there are no large terrestrial predators present in the area.

The vegetation is diverse and ranges from polar desert with extremely low plant cover to relatively dense *Dupontia* marshes. Ridge communities largely remain snow-free during winter, contain very few species, and are characterized by the presence of *Dryas octopetala* L. and *Salix polaris* Wahlenb. Extensive heathland areas (*Luzula* heath) occur, which are dominated by *Luzula confusa* Wahlenb. and *Salix polaris* Wahlenb., and in wetter places also *Alopecurus borealis* Trin. (*Luzula-Alopecurus* heath). On shallow slopes, patches of graminoid vegetation are found, with a relatively high density of grasses, including *Poa alpigena* Lindm., *P. alpina* L., *Festuca cryophila* V. I. Krecz. & Bobrov and *Alopecurus borealis* Trin. Wet moss vegetation is characterized by *A. alpinus* and a relatively high density of *Equisetum arvense* L. *Dupontia* marshes hold numerous species, but are dominated by *Dupontia* spp. and *Eriophorum scheuchzeri* Hoppe (van der Wal *et al.* 2000a).

RUMEN SAMPLES AND CARCASS MEASURES

Rumen content was sampled from 117 females culled for scientific purposes between 1998 and 2004. All animals were culled between 16 September and 11 December, and age ranged from 2 to 17 years when permanent teeth are fully erupted (Table S1 in Supplementary material). A sample of 300–500 ml of rumen content was obtained by sampling spoonfuls from various locations of the opened rumen immediately after culling. The samples were then kept frozen at –20 °C for later analysis. Sex and dressed weight were recorded from all animals shot. Animal age was determined by sectioning incisors and counting cementum annuli (Hamlin *et al.* 2000).

PARTICLE SIZE DISTRIBUTION

Size distribution of plant fragments was determined by wet sieving. Thawed rumen contents were mixed thoroughly and subsamples of 120 ml were washed with water into sieve trays (200 mm) with square pores of 8·0, 4·0, 2·0, 1·0, 0·5, 0·25 and 0·1 mm. Particles passing the 0·1 mm sieve were discarded. The sieve stack was attached to a Labotron benchtop orbital shaker (type AK 15; Infors HT, Bottmingen, Germany) and shaken at 125 r.p.m. while water was sprayed gently from a handheld shower until fractioning was completed. All material left on each sieve was transferred to predried and weighed Petri dishes, and dried at 105 °C to constant weight. The dried material from each sieve was then calculated as a proportion of the total dry matter retained from all sieves.

TOOTH MEASUREMENTS

Recent developments in computerized scanning imaging technologies combined with powerful image-analysis software have made it possible to represent and interpret three-dimensional objects (Evans, Harper & Sanson 2001; Scott *et al.* 2005). Dried and cleaned jawbones from 48 females, ages ranging from 2 to 11 years, were presented for scanning (Table S2). The occlusal surface of M1 was digitized using structured light projection. This is a triangulation-based optical 3-D shape-measurement technique (Sansoni, Carocci & Rodella 1999). A data projector is used to illuminate the object under measurement with a sequence of light patterns. The object is observed with a video camera placed at an angle with regard to the direction of projection. In each pixel of the camera, the observed intensities in the sequence make up an optical 'code' that can be processed to yield the height of the object. A telecentric camera objective ensures that the influence of perspective is minimal, and lateral pixel size can be determined with standard camera calibration techniques. The field of view was set to ≈40 × 30 mm with a lateral resolution of 0·055 mm. Calibrated height range was ≈24 mm and the height accuracy 0·01 mm.

The shininess and transparency of enamel can cause considerable measuring errors when using structured light projection. To avoid this problem, the occlusal surface was sprayed with a developer, producing a fine and even coating of the surface examined. Measurements, resulting in a matrix of height values, were controlled by the HOLOVISION software (developed at SINTEF ICT, Department of Optical Measurement Systems and Data Analysis) before read in to MATLAB for further processing. This direct link between the scanning procedure and analytical software allowed immediate quality assurance of all scans.

TOOTH TOPOGRAPHY INDEX

Assuming that any deviation from a flat surface will improve the cutting and grinding efficiency of a herbivore molar, we calculated an index that expressed the topographic variation of the occlusal surface. A cross-sectional tooth profile was extracted along the line describing the maximum width of the posterior moiety of M1 (Fig. 1). The digitized tooth profiles were saved as ASCII files and imported into the statistical software package R (R Development Core Team 2006). The total length of the curved occlusal surface line (CL) was calculated by summing distances between individual data points (resolution 0·055 mm) from the outer buccal to the inner lingual enamel edge. Simultaneously, the length of the straight line (SL) between the defined inner and outer enamel edge points was calculated. The occlusal topographic variation index (TVI) was then calculated by dividing CL by SL (Fig. 1). Higher index values express a more rugged tooth than lower values. To enable measurement of tooth height from the tooth profiles, a
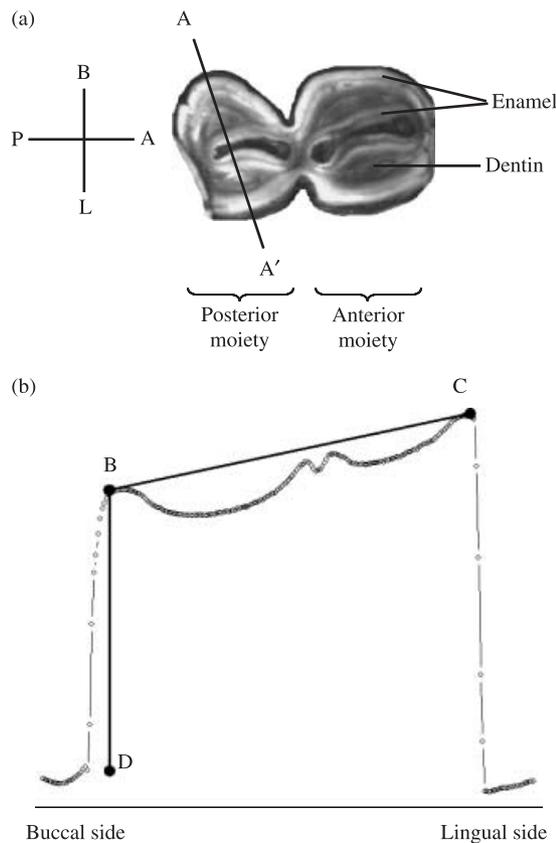
(a)

A

B

P — A

L

Enamel

Dentin

A′

Posterior moiety   Anterior moiety

(b)

C

B

D

Buccal side   Lingual side

Fig. 1. A cross-sectional tooth profile was extracted from the digitized photos along the line A–A′ describing the maximum width of the posterior moiety of M1 (a). Information from this profile (b) was used to calculate the occlusal topographic variation index (TVI). B and C represent the buccal and lingual enamel edges, respectively, and the straight line (SL) drawn between these two points corresponds to the imaginary occlusal surface line expected to be of least chewing efficiency. The actual occlusal tooth surface is visualized as the curved, dotted line (CL) between B and C. Tooth height was calculated as the distance from the buccal enamel edge (B) to the jaw bone (D).

piece of Blu Tack was attached to the jawbone at the buccal and lingual base of the tooth being scanned. On the extracted tooth profiles, the Blu Tack pieces appeared as the horizontal baselines, and tooth height was then measured on the buccal side as the distance from the baseline to the enamel edge.

ANALYSES OF DIET COMPOSITION AS A MEASURE OF PLANT QUALITY

Botanical composition analyses of rumen samples were carried out by a point-identification method (Gaare, Sorensen & White 1977). Each rumen sample was thawed and homogenized by stirring before four subsamples of ≈50 ml were collected. Each subsample was washed onto a circular sieve with a diameter of 19 cm and a mesh size of 2 mm. Particles escaping through the sieve were discarded. A 1·6-cm grid was marked on the mesh, and for every subsample, 100 plant fragment identifications were carried out through

a stereomicroscope at grid intersections. Overall, 93·7% (±1·4) of all plant fragments were identified to species or species group. The proportion of every species or species group found in rumen samples from one individual was calculated according to equation 1, a being a particular species or species group and a_i being the number of plant fragments belonging to this class in subsample i.

$$\text{Proportion } a = \frac{\sum_{i=1}^{4} a_i}{400} \qquad \text{eqn 1}$$

Diet composition analyses were available only for animals shot in the Colesdalen/Semmeldalen area ($n = 66$, Table S3).

STATISTICAL ANALYSES

Passage of particles through the reticulo-omasal orifice is size-limited, and thought to be quite similar for most ruminants, being ≈1 mm for sheep and 1–2 mm for cattle (Reid, Post & Titchen 1991). As a response variable, we therefore used (arcsine[sqrt]) proportion of particle sizes <1·0 mm (hereafter termed small particles) of the total amount of dried particles retrieved from all the size fractions. Note that results did not differ qualitatively if we used the 0·5 or 2 mm fraction as the upper limit for particles.

Overall, the winter diet of Svalbard reindeer consisted of 66·7% graminoids, 3·2% forbs, 11·1% shrubs, 10·5% mosses, 0·8% lichens, 1·2% *Equisetum* sp. and 6·3% unidentified items or hair. Our aim was not to describe diet composition as such, but to identify if diet quality and diet composition affect our primary variables particle size and tooth wear. We considered two approaches to find covariates we could use as meaningful measures of diet quality and diet composition, respectively: (1) proportion of high-quality plants in diet; and (2) first axis of a PCA of diet composition. (1) According to earlier studies of digestibility and nutritional content in common Svalbard reindeer forage plants (Staaland *et al.* 1983), most graminoids, forbs and shrubs utilized as forage are known to be highly digestible, at least during summer. The proportion of graminoids, forbs and shrubs varied among individuals between 53·3 and 96·5%. We therefore used proportion of graminoids, forbs and shrubs as an index of variation in diet quality between individuals. (2) Variation in quality may exist within plant species pooled as graminoids, forbs or shrubs. We therefore identified nine major plant species, families or groups in the diet (*Alopecurus borealis* Trin., *Eriophorum scheuchzeri* Hoppe., *Trisetum spicatum* L., *Dupontia*, *Luzula*, *Poa* & *Festuca rubra* L. *arctica*, unclassified graminoids, *Salix polaris* Wahlenb. and bryophytes), that were all found to represent 10% or more in at least one rumen sample. As an index of overall diet composition, we used the first axis of a principal components analysis (PCA), which explained 36% of the variation in diet composition.

Table 1. Parameter estimates for variation in the proportion of small particles (<1·0 mm) in the rumen of Svalbard reindeer obtained from the most parsimonious linear model (least-squares estimates) and from 1000 parametric bootstrap replicates, with bootstrapped SE and CI

	LS estimate	Bootstrap estimate	Bootstrap SE	Bootstrap 95% CI	
				Lower limit	Upper limit
Intercept	0·84081	0·84082	0·01781	0·80519	0·87644
Age	0·00745	0·00747	0·00537	−0·00327	0·01820
(Age)^2	−0·00089	−0·00089	0·00034	−0·00157	−0·00021
Sub-population (Sassen vs. Colesdalen/Reindalen)	−0·01456	−0·01450	0·00571	−0·02591	−0·00308
Year (1999 vs. 1998)	−0·00044	−0·00059	0·00911	−0·01880	0·01762
Year (2000 vs. 1998)	−0·02632	−0·02618	0·00519	−0·03656	−0·01580
Year (2001 vs. 1998)	−0·00061	−0·00062	0·00316	−0·00694	0·00570
Year (2002 vs. 1998)	−0·01270	−0·01287	0·00251	−0·01789	−0·00784
Year (2003 vs. 1998)	−0·01158	−0·01157	0·00247	−0·01651	−0·00663
Year (2004 vs. 1998)	0·00724	0·00724	0·00244	0·00235	0·01213

Reference levels for factors 'Year' and 'Sub-population' are 1998 and Colesdalen/Reindalen, respectively ($N = 117$, $r^2 = 0·47$). All animals were culled in the period between 16 September and 11 December.

We used generalized additive models (GAM, Hastie & Tibshirani 1999) to explore non-linearity in the relationships between age, body mass, TVI, diet composition and particle size. For GAM modelling, we used the library 'mgcv' in R (Wood 2006), as it allows inclusion of interactions between continuous variables. Thereafter we used linear models (LMs) to parameterize linear (including curve-linear) relationships between the same variables. Body masses were ln-transformed to make the relationship of the response variable more linear and to stabilize the variance.

To compare LMs, we used the Akaike information criteria corrected for small samples, AIC$_c$ (Burnham & Anderson 2002), which represents a compromise between fit and the number of factors entered in the model (the parsimonious principle). We were mainly interested in effects of age and body mass (and their possible interactions, cf. H1–3). Body mass was standardized by dividing individual deviation from mean (ln) body mass by SD (ln) body mass. In addition, the continuous weight loss during winter was corrected for by controlling for date of culling. As there was some imbalanced sampling among years and subpopulations (Tables S1 and S2), we always kept these factors in the model, irrespective of fit, to control for potential bias. In addition, we bootstrapped the residuals from the most parsimonious LMs investigating the bias between the bootstrapped means and our sample means. We also confirmed that the confidence intervals derived from our sample and the bootstrapping procedure did not lead to conflicting inferences (Efron & Tibshirani 1998).

Analyses were performed using the statistical packages R and SPLUS.

Results

The proportion of small particles in the rumen of Svalbard reindeer decreased with increasing age in all models (supporting H1; Table 1, Fig. 2). The most parsimonious
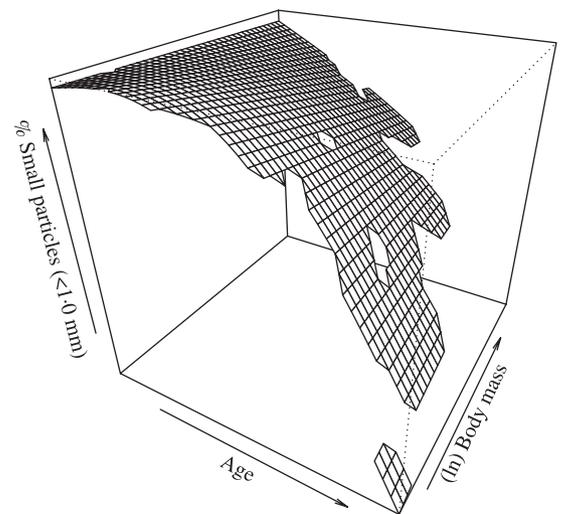

Fig. 2. The plotted GAM for the arcsine(sqrt) proportion of small particles (<1·0 mm) in the rumen of female Svalbard reindeer as a response of the interaction between age (year) (ln) body mass for 117 animals ranging from 2 to 17 years old (df = 3 for the smoothing spline).

model included a second-order polynomial term for age (AIC$_c$ = −349·470). An extended model containing the additional first-order term of body mass (ΔAIC$_c$ = 1·567) was fairly competitive (Table S4), although body mass did not come out as significant when estimating its effect, thus rejecting H2. Animals shot in Sassendalen had significantly more large particles in their rumens than animals shot in the Colesdalen/Semmeldalen area ($t = -2·442$, $P = 0·016$), and the proportion of small rumen particles varied between years (Table 1). The inclusion of the diet quality or composition (proportion of graminoids, forbs and shrubs, estimate = −0·22747 [−0·43075, −0·02419]; first axis of PCA, estimate = 0·01242 [0·00041, 0·02442]) as a covariate did not alter the estimated effects of age (age: estimate = 0·01471 [0·00048, 0·02893]; (age)^2: estimate = −0·00145 [−0·00240, −0·00050]).

Table 2. Test summaries for the best linear models describing variation in the occlusal topographic variation index (TVI) and in tooth height (*N* = 48)

	LS estimate	Bootstrap estimate	Bootstrap SE	Bootstrap 95% CI	
				Lower limit	Upper limit
TVI					
Intercept	1·3038	1·30322	0·04323	1·21677	1·38967
Age	−0·0187	−0·01863	0·00548	−0·02958	−0·00768
st(ln[Body mass])	−0·0299	−0·02993	0·01608	−0·06210	0·00224
Sub-population (Sassen vs. Colesdalen/Reindalen)	−0·0854	−0·08578	0·03938	−0·16454	−0·00702
Year (2002 vs. 2001)	−0·0151	−0·01421	0·04241	−0·09902	0·07060
Year (2003 vs. 2001)	−0·0255	−0·02449	0·04536	−0·11521	0·06623
Year (2004 vs. 2001)	−0·0555	−0·05517	0·04756	−0·15028	0·03994
Tooth height					
Intercept	11·4505	11·42877	0·64532	10·13813	12·71941
Age	−0·8647	−0·85713	0·22560	−1·30833	−0·40593
(Age)^2	0·0323	0·03165	0·01813	−0·00461	0·06791
st(ln[Body mass])	−0·9193	−0·92396	0·30098	−1·52592	−0·32200
st(ln[Body mass])^2	−0·2305	−0·23015	0·11324	−0·45663	−0·00367
Age × st(ln[Body mass])	0·1658	0·16692	0·05495	0·05702	0·27682
Sub-population (Sassen vs. Colesdalen/Reindalen)	−0·3595	−0·36344	0·18764	−0·73872	0·01184
Year (2002 vs. 2001)	0·0749	0·07668	0·19530	−0·31392	0·46728
Year (2003 vs. 2001)	0·1175	0·11487	0·09639	−0·07791	0·30765
Year (2004 vs. 2001)	−0·0137	−0·01578	0·08526	−0·18630	0·15474

Parameter estimates are given as least-squares estimates for the linear models and estimates, SE and CI from 1000 parametric bootstrap replicates. Reference levels for factors 'Year' and 'Sub-population' are 2001 and Colesdalen/Reindalen, respectively. St(ln[Body mass]) = standardized ln-transformed animal body mass.

Data on tooth topography were derived from a subset (*n* = 48), and as age and tooth topography are highly correlated, we used model selection for inference. The best model explaining variation in tooth topography contained body mass and up to a third-order polynomial term of age. The topography of the tooth became less rugged as they aged, and heavier individuals had less rugged molars than lighter ones (Table 2). Plotting the best model revealed that, within younger age groups, the molar surface of lighter individuals was generally more rugged (a higher TVI value) than for heavier individuals (Fig. 3). This supports H3, as heavier animals under a given set of nutritional conditions are expected to have processed more food, resulting in increased tooth wear, than lighter individuals of the same age. Several other models, consisting of lower-order terms of age, second order terms of body mass and their first-order interaction, were competitive (ΔAIC$_c$ < 2; Table S5). Using GAM, the model including the interaction term between age and body mass was slightly better (AIC$_c$ = −72·939) than the model with only additive effects of age and body mass (ΔAIC$_c$ = 0·804). Both analyses thus clearly showed that TVI was related to both age and body mass, while there was more marginal evidence that the effect of body mass decreased with age. Including the proportion of graminoids, forbs and shrubs in the diet (estimate = −0·15471 [−0·65867, 0·34925]; *n* = 33) or first axis of the PCA (estimate = 0·00868 [−0·02055,
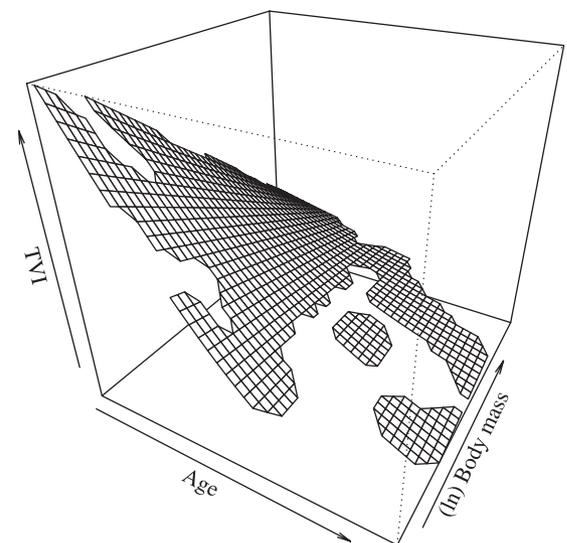

Fig. 3. The plotted GAM for the occlusal topographic variation index (TVI) as a response of the interaction between animal age (year) and (ln) body mass for 48 animals ranging from 2 to 11 years old (df = 3 for the smoothing spline).

0·03728]; *n* = 33) as a covariate, did not affect the estimate for age (−0·01653 [−0·02977, −0·00329]), but increased the estimate for the negative effect of (ln) body mass (−0·11192 [−0·02977, −0·00329]). Although tooth height decreased with age, the best LM describing

tooth-height variation consisted of both second-order polynomial terms for age and body mass in addition to more complex interaction terms for these variables (Table S6).

Our last question was whether tooth wear (TVI) provided a better predictor of rumen particle size than both age and tooth height. The best model from the analysis related to occurrence of small rumen particles (Table S4) was run with the subset containing additional data on TVI and tooth height (AIC$_c$ = −131·146 for age + age^2; see Table 2 for parameter estimates). While tooth height performed approximately equal to this model (ΔAIC$_c$ = 0·284), replacing the age terms with TVI provided a slightly better model (ΔAIC$_c$ = −1·511). As predicted from H1, this indicates that tooth topography is responsible for the age effect, and provides a better predictor of rumen particle size than age.

Discussion

We provide the first evidence of a trade-off between fast early growth and wear (a somatic cost) of a senescence-related trait – the structure and height of the molar – in a wild ruminant. Up to ≈5 years old (Fig. 3), heavier females of Svalbard reindeer had more worn teeth than lighter ones (consistent with H3). This is the first evidence from a contemporary ruminant population suggesting a selection pressure for hypsodonty, as would be expected in dry climates with sparse vegetation (Fortelius *et al.* 2002), such as arid ecosystems and also the extreme arctic desert on Svalbard.

THE TOOTH WEAR CONSTRAINT HYPOTHESIS (H1) VS. THE ALLOMETRY, OPTIMALITY HYPOTHESIS (H2)

Although teeth contain the most durable of all biological tissues, gradual deterioration from wear is inevitably causing alteration of occlusal structure and in turn affecting grinding capacity (Lanyon & Sanson 1986; Perez-Barberia & Gordon 1998b; Logan 2003). By measuring chewing investment, occlusal surface area and average particle size found in faeces, Perez-Barberia & Gordon (1998b) estimated tooth effectiveness in a group of 12 female red deer (*Cervus elaphus* L.) ranging from 4 to 25 years old. Despite their small sample size, they found that prime-aged individuals had a larger occlusal surface area and were more efficient in reducing forage particle size in faeces than both younger and older individuals. This relationship supports Luke & Lucas's (1983) arguments proposing that teeth of most herbivores rely on a moderate amount of wear to attain a functional shape. Once this has been achieved, the tooth is constructed so that shape and function are maintained for much of its life, despite the large amount of wear (Rensberger 1988). Such a persistent maintenance of molar function was not found for Svalbard reindeer. Clearly, rumen content is a mixture of recently ingested forage and material already masti-

cated through subsequent rumination bouts, but we found that diet composition or quality had no marked effect on the reported patterns of particle size. Some authors have used particle size in faeces as a measure of chewing efficiency (e.g. Perez-Barberia & Gordon 1998b), and whether results may depend on particles being used in rumen or faeces remains to be established with certainty.

In accordance with earlier studies regarding molar height (Skogland 1988; Kojola *et al.* 1998; Loe *et al.* 2003), age was clearly the most important predictor for variation in tooth height and occlusal tooth topography (TVI). This age-related decrease in TVI caused a significant reduction in tooth efficiency leading to a gradual decrease in the proportion of small rumen particles irrespective of body mass (supporting H1). A clear reduction in subcutaneous fat depositions with increasing age (V.V., unpublished data) also suggests that reduced chewing efficiency directly affects the amount of energy stored, and subsequently the animals' ability to overcome periods of starvation. The occlusal surface among heavier animals of age classes up to around 5 years was consistently more worn (lower TVI values) compared with lighter animals of the same age. Despite this, larger individuals tended to have a larger proportion of small rumen particles, contrary to expectations from allometric relations (H2). Enhanced tooth wear at younger ages as a potential consequence of an early growth investment may be partly compensated by increased mastication effort causing rumen particle size distribution to remain fairly constant, irrespective of animal body mass (rejecting H2).

For the studies not using tooth height as a measure of tooth wear, the most frequently used measures of tooth effectiveness are occlusal surface area, molar occlusal contact area and length of enamel cutting edges of the occlusal surface (see review by Perez-Barberia & Gordon 1998a). These measures aim at providing direct quantitative information about variation in tooth effectiveness. This was also the aim for our occlusal TVI. Based on the assumption that Svalbard reindeer teeth wear in a predictable way, and that any deviation from a plain surface would assist the forage grinding process, the index includes the most relevant information regarding variation in tooth efficiency. This assumption was supported as TVI was a slightly better predictor for the proportion of small rumen particles than tooth height or any combination of age, body mass and their interactions. This provided further support for H1.

THE GROWTH-INVESTMENT HYPOTHESIS (H3)

Heavier individuals of a species typically perform better than lighter ones, as evidenced from patterns of juvenile survival (Festa-Bianchet *et al.* 1997), age at first reproduction (Langvatn *et al.* 2004), and longevity (Gaillard *et al.* 2000). These high-quality individuals tend to both start reproducing earlier and live longer

than inferior individuals (Weladji *et al*. 2006), demonstrating life-history trade-offs in large mammals has often proven difficult. However, few studies have explicitly addressed the possible trade-off between a short-term process such as mastication (increased energy extraction from ingested forage) and a future or longer-term process such as the effect of tooth wear (reduced chewing efficiency).

In order to grow faster or maintain a higher body mass, larger animals either have to process more forage, eat a higher quality diet, or prolong rumen retention time in order to increase intake of metabolizable energy compared with smaller individuals. Due to the sparse vegetation at this exceptionally high latitude, it has been demonstrated that the energy intake of Svalbard reindeer is restricted more by limitations regarding forage quantity, rather than quality (van der Wal *et al*. 2000b). Therefore, in Svalbard reindeer, increases in metabolizable energy intake, faster growth and higher body mass are most likely to be related to increased food intake, causing increased processing effort. Within age groups, heavier animals are therefore expected to have experienced a higher molar wear rate than lighter ones.

SELECTION FOR HYPSODONTY

If tooth height in itself was the single proximate cause of senescence, evolution would probably lead to strong directional selection on this trait and thereby generally stabilize its influence (Williams 1957). Indeed, initial molar height in male and female red deer are linked to expected longevity (Carranza *et al*. 2004). Although hypsodonty as an adaptation for wear tolerance has been firmly linked to dry climate (Fortelius 1985; Janis 1988; Fortelius *et al*. 2002), the mechanisms remain elusive. Plant quality as a factor seems to differ. In arid ecosystems, plant quality is low due to increased fibrousness and decreased nutritive value (Fortelius *et al*. 2002). In contrast, plant quality in the arctic is high (van der Wal *et al*. 2000b). Increased abrasiveness due to extraneous dust can therefore be an important link to evolution for hypsodonty in dry habitats. Both arid ecosystems and the arctic desert on Svalbard are sparsely vegetated. Limited vegetation coverage and low-growing plant species easily lead to ingestion of sand particles together with the forage. We suggest that the trade-off between early growth and increased tooth wear in Svalbard reindeer is due to the extreme foraging conditions experienced in the arctic desert, which may be more extreme than the environment in which reindeer evolved. It remains unclear whether extraneous dust can be a single cause of selection for hypsodonty. Increased tooth wear was also found in the elk population inhabiting the Madison river drainage of Yellowstone National Park (Garrott *et al*. 2002). Geochemical processes caused elevated levels of fluorine and SiO_2 (Garrott *et al*. 2002) in vegetation and water. While the high exposure to fluorine caused compromised

dentition due to fluoride toxicosis, molar wear was further accelerated by the abrasive action of silica (Garrott *et al*. 2002). The increased molar wear rates caused an earlier onset of survival senescence, subsequently altering the demographic population structure. Thus important insight into the role of tooth wear for life history may derive from areas where animals are foraging in environments more extreme than where they evolved.

Acknowledgements

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Supplementary material

The following supplementary material is available for this article.

Table S1. Rumen samples were collected from 117 Svalbard reindeer culled for scientific purposes between 1998 and 2004 in the two areas Colesdalen/Reindalen and Sassendalen.

Table S2. Year of culling and age distribution of 48 animals from which information about molar wear and tooth height was collected.

Table S3. Rumen samples from 66 Svalbard reindeer were analysed for botanical composition.

Table S4. Results from model selection on the response variable (arcsine square root transformed) proportion of small particles in the rumen of Svalbard reindeer (the best model in bolded fonts).

Table S5. Results from model selection on the response variable TVI (the occlusal topographic variation index) in Svalbard reindeer (the best model in bolded fonts).

Table S6. Results from model selection on the response variable tooth height in the Svalbard reindeer (the best model in bolded fonts).