

Leif Egil Loe · Christophe Bonenfant · Rolf Langvatn
Atle Mysterud · Vebjørn Veiberg · Nils Chr. Stenseth

Increased effect of harsh climate in red deer with a poor set of teeth

Received: 21 January 2005 / Accepted: 23 May 2005 / Published online: 10 December 2005
© Springer-Verlag 2005

Abstract Teeth are vital for mammal performance and especially in ungulates relying on mechanical decomposition of plant material for effective microbial digestion and energy uptake. The main focus of the role of teeth in ungulate life histories has been on tooth wear, while no one has addressed to what extent deviation from the natural set of teeth (malocclusion) causes variation in individual fitness components. Based on mandibles from 41,066 individual red deer (*Cervus elaphus* L.) collected from 1969 to 2001, we tested whether malocclusion had an effect on individual body condition and whether this effect depended on environmental harshness. Females with malocclusion (0.6% of the population) were in a poorer condition than individuals without tooth anomalies and the effect increased during unfavorable climatic conditions. The effect of malocclusion in males was less clear. This study indicates that a well-functioning set of teeth is essential for mammal performance, and that selection pressure against (dental) anomalies is more pronounced when climate is unfavorable.

Keywords Dentition · NAO · Ungulates · Body weight · Mechanisms

Electronic Supplementary Material Supplementary material is available for this article at <http://dx.doi.org/10.1007/s00442-005-0172-7>

L. E. Loe · C. Bonenfant · A. Mysterud (✉) · V. Veiberg
N. Chr. Stenseth
Centre for Ecological and Evolutionary Synthesis (CEES),
Department of Biology, University of Oslo, P.O. Box 1066,
Blindern, 0316 Oslo, Norway
E-mail: atle.mysterud@bio.uio.no
Tel.: +47-22-854045
Fax: +47-22-854726

R. Langvatn · V. Veiberg
The University Centre in Svalbard (UNIS),
9170 Longyearbyen, Spitsbergen, Norway

R. Langvatn
Norwegian Institute for Nature Research,
Tungasletta 2, 7005 Trondheim, Norway

Introduction

Mammals depend on a well-functioning set of teeth to acquire and process food. This is particularly critical for ungulates where effective energy absorption in the digestive tract depends on the molariform teeth's ability to reduce plant particle size to ensure more efficient microbial digestion (Pérez-Barbería and Gordon 1998). Size and form of the front teeth (in addition to muzzle width) may also affect a herbivore's ability to select the preferred forage plants (Gordon and Illius 1988). Recent studies have investigated the importance of tooth wear for the life history of ungulates (Skogland 1988; Ericsson and Wallin 2001; Loe et al. 2003). Malocclusion (i.e., deviation from the natural set of teeth) is likely to reduce teeth function to a higher extent than wear. Decreased longevity was found in elk *Cervus elaphus* with severe tooth damages due to anomalous exposure to fluoride and silica (Garrott et al. 2002). Only two large-scale studies (Zima 1988; Azorit et al. 2002) have reported frequency of malocclusion occurrence in natural populations of ungulates (but see, e.g., Kierdorf and Kierdorf 2002 for single individuals) and no study has so far investigated the consequences of tooth anomalies for ungulate life history under more normal conditions (than those present in the study system of Garrott et al. 2002).

In general, the environment affects life history traits (such as condition, fecundity, and survival) in ungulates (Coulson et al. 2000), but inferior and injured individuals may suffer even more from environmental stress than 'normal' individuals. In the specific case of malocclusion, individuals with inferior teeth may suffer more at high population density and/or under adverse climatic conditions (especially if there is a deep snow layer), if malocclusion were related to their poorer ability to masticate sub-optimal diets composed of rougher items. Anomalies may accumulate throughout life and become progressively more important for individual performance as they age.

Here, we report on the age- and sex-specific frequency of malocclusion in a sample of 41,066 Norwegian red deer (*Cervus elaphus* L.). We check if the frequency of tooth anomalies increases by age. Thereafter, we test for the first time the hypotheses that body condition is lower in red deer with malocclusion, and that this is more pronounced at a high population density and during unfavorable climatic conditions.

Materials and methods

Study area

The study area consists of 65 municipalities covering large parts of the Norwegian south–west coast, which is the main area for red deer in Norway (Langvatn et al. 1996). Red deer in the study area can be divided into five populations corresponding to Norwegian counties: Rogaland and Hordaland (P1), Sogn og Fjordane (P2), Møre og Romsdal and Sør-Trøndelag (P3), Nord-Trøndelag (P4), and the island Hitra (P5; Mysterud et al. 2000). Red deer eat graminoids and herbs in summer and prefer blueberry and cowberry (*Vaccinium* L. sp.) in the winter. However, when the snow layer is deep they no longer have access to these dwarf shrubs and change to browse and bark stripping in the tree layer (aspen (*Populus tremula* L.), rowan (*Sorbus aucuparia* L.), willow (*Salix* L. sp.), juniper (*Juniperus communis* L.), and Scots pine (*Pinus sylvestris* L.) (Ahlén 1965; Ahlén 1975).

Red deer data

A total of 41,066 mandibles from adult red deer (>1 year old) were sampled during the annual autumn harvest 1969–2001 (between 10th September and 15th November), together with data on body weight and records of date of culling and locality (municipality) (Langvatn et al. 1996). Recorded body weight is dressed weight (accounting for 58% of live weight; Langvatn 1977). Jaw length was measured according to Langvatn 1977). Age was estimated from annual tooth cementum layers (Mitchell 1967; Reimers and Nordby 1968).

Dental abnormalities were classified according to the involved teeth and the malformation type (Table 1). The various types of malocclusion are a combination of innate anomalies and mechanical damages inflicted throughout life. Due to the relatively low number of individuals with tooth anomalies, we did not attempt to analyze subsets of specific types of teeth nor specific type of anomalies (listed in Table 1). We found that the origin and the age of a tooth anomaly (i.e., if it was innate or inflicted) could not be established for the majority of individuals. Hence, we do not separate ‘innate’ or ‘inflicted’ tooth anomalies in the following analyses. Teeth can sometimes be lost from cleaned, dry jaws, or fracture during improper handling of mandibles. These

post-mortem changes were distinguished from ante-mortem ones by looking at the alveoli and by the condition of the tooth fracture planes.

Environmental covariates

In an average year, snow covers the ground from December to March; however, snow cover is dependent on altitude and phase of the North Atlantic Oscillation (see Hurrell and Van Loon 1997 for definition of the NAO). On the west coast of Norway, high NAO values in winter correlate with high temperatures and much precipitation (falling mainly as rain at low elevation, and more often as snow at high elevation). In lowland red deer wintering areas, a significant snow cover is only present in years with low NAO value (Mysterud et al. 2000). We used the mean NAO value from December to March as a covariate in our analyses. Recently, the use of large-scale weather packages (such as the NAO) has been acknowledged to predict ecological processes better than local climate in some cases (Hallett et al. 2004).

In order to obtain an index for population density in a given year and municipality, we divided the total number of harvested red deer on the ‘qualifying area’, which is the area defined as deer habitat by the management authorities (see Mysterud et al. 2001c for details).

Statistical analyses

Frequency of tooth anomalies

Tooth anomaly occurrence was modeled as a binary response (present or not) using the Generalized Linear Model with a logit link and binomial error distribution (McCullagh and Nelder 1989; Agresti 1990). However, given the relatively low occurrence of malocclusion in red deer (>1% in average), standard logistic regression might give biased results (McCullagh and Nelder 1989; Venables and Ripley 1999) by underestimating the probabilities of the studied event to happen (King and Zeng 2001). A way to overcome such biases is to modify the maximum likelihood estimator (Firth 1993; Heinze and Schemper 2002), which bears the consequence that we could not compute the Akaike Information Criterion (AIC; Akaike 1974) required for the theoretical information approach as we did in the body mass analyses included in this paper. As recommended for the modeling of rare events such as tooth anomalies, profile likelihoods were used to test the effect of year, population, sex, and age on tooth anomaly occurrence (Venables and Ripley 1999; Heinze and Schemper 2002). Finally, we assessed the model fit (goodness-of-fit tests, GOF) according to Agresti (1990) by (1) transforming continuous variables into an 8-class categorical variable and (2) comparing the Pearson residuals with a Chi-square with the residual number of degrees of freedom.

Table 1 Occurrence of the different types of malocclusion in molars, premolars, and incisors of female and male Norwegian red deer

	Molars		Premolars		Incisors		Total	
	<i>n</i>	Percentage	<i>n</i>	Percentage	<i>n</i>	Percentage	<i>n</i>	Percentage
Females								
No malocclusion	16,773	99.87	16,735	99.65	16,760	99.84	16,735	99.36
Missing ^a	5	0.03	38	0.23	5	0.03	48	0.28
Broken ^b	0	0.00	1	0.01	10	0.06	11	0.07
Malocclusion (incl torsion)	4	0.02	6	0.04	9	0.05	19	0.11
Supernumerary teeth	1	0.01	1	0.01	1	0.01	3	0.02
Not specified/Other	12	0.08	13	0.08	2	0.02	27	0.16
Males								
No malocclusion	24,134	99.93	24,104	99.79	24,104	99.79	24,104	99.51
Missing ^a	3	0.01	23	0.10	6	0.02	32	0.13
Broken ^b	2	0.01	2	0.01	5	0.02	9	0.04
Malocclusion (incl torsion)	1	0.00	4	0.02	24	0.10	29	0.12
Supernumerary teeth		0.00	5	0.02	1	0.00	6	0.02
Not specified/Other	11	0.04	17	0.07	15	0.06	43	0.18

^aNo visible remains

^bVisible remains of the tooth

We assume that a good fit of simple models (including only one predictor variable) indicates that extended models also fit well (as done in Langvatn et al. 2004). All GOF *P*-values were > 0.4 , suggesting that the models captured the data adequately.

Body weight analyses

The effects of malocclusion on log-transformed (to stabilize variance) body weight were investigated with the Generalized Linear Model (McCullagh and Nelder 1989) using an identity link function and a normal error distribution. All factors shown earlier to affect red deer body weight were included in our initial model (see Yoccoz et al. 2002; Loe et al. 2003 for a similar approach). These variables were age (as 5 age classes for females and a 6-order polynomial function for males; Myrsterud et al. 2001c), density (Myrsterud et al. 2001c), the NAO (Myrsterud et al. 2001b), latitude (Myrsterud et al. 2001a), diversity of aspect (with the Shannon-Wiener information criteria; data: proportion of area facing north, northeast, east, southeast, south, southwest, west, and northwest in each municipality), proportion of high altitude habitat and the distance to the coast (Myrsterud et al. 2001a), and population (Myrsterud et al. 2001a). Second-order interactions between population, age, and the NAO were also entered in the model. We followed the same procedure as Yoccoz et al. (2002) and standardized covariables so that coefficients could be easily interpreted as well as allowing the comparison of the relative strength of each covariable.

The model selection was based on the Akaike Information Criterion (AIC), which selects the most parsimonious model. We followed the information theoretic and model averaging approaches (Burnham and Anderson 1998) which include more than one single best model. This procedure has recently been promoted as a useful tool in evolutionary biology and ecology for

studies based on observational data (Johnson and Omland 2004), although it inflates the standard errors of parameter estimates. An example of this model averaging procedure in ecology is given by Conner et al. (2001). From model AICs, we derived the relative AIC weights as

$$\hat{w}_i = \frac{e^{-0.5 \times \Delta \text{AIC}_i}}{\sum_{j=1}^k e^{-0.5 \times \Delta \text{AIC}_j}},$$

which gives the probability for the model *i* to be the best model. This model averaging procedure thus accounts for the model selection uncertainty that is an integrated part of the statistical inference (Buckland et al. 1997). We considered a set of best models including all models within a range of four AIC points from the best model to build up the average model. The average model estimates were estimated as the weighted mean (\hat{w}_i) of the set of best model coefficients. Coefficient variances were calculated as

$$\text{var} \beta_j = \sum_{i=1}^k \hat{w}_i \sqrt{\text{var}(\beta_{j,i}) + (\beta_j + \bar{\beta})^2},$$

where β_j is the coefficient of interest and $\beta_{j,i}$ the estimate of β_j knowing model *i* (Burnham and Anderson 1998). According to Burnham and Anderson (1998), these average model estimates of the coefficients are lowered to 0 and have increased variance when they do not appear in the *i*th model. Hence, some variables may be selected in the average model without being significantly different from 0.

We assessed independent probability for the *i*th model to be the best model using a bootstrap resampling method (Efron and Tibshirani 1993) denoted as π_i (Buckland et al. 1997; Burnham and Anderson 1998) by analyzing resamples and selecting the model as done in the original data. We ran 10,000 bootstrap batches

(treating each observation as independent) to test the reliability of the standard AIC model selection.

As we used log body weight as the response variable in all analyses, one may argue that the causal relationship between malocclusion and phenotypic quality cannot be established in transversal data when using body weight as response. Individuals may become small as a result of tooth anomalies, or they may get tooth anomalies as a consequence of their lower phenotypic quality. We therefore included a measure of skeletal body size (jaw length) as a predictor so that the effect of malocclusion on body weight after skeletal body size is accounted for can be interpreted as an effect on body condition. Body condition is much less likely to influence malocclusion than the other way around, avoiding a discussion of causality in our results. However, we also performed the analyses without including jaw length and this gave qualitatively the same results.

All analyses were performed in S-Plus (Insightful, Seattle, WA, USA) and R (R Development Core Team 2004).

Results

The overall frequency of any type of malocclusion in Norwegian red deer was 0.6% for females and 0.5% for males (Table 1). The frequency of malocclusion increased by age both in females and males (from less than 0.5% in young age classes to more than 6% in the oldest females; Fig. 1), indicating that most of the damages in the old individuals are not innate, but have accumulated throughout life. There was no main effect of sex (estimate = 0.3411, SE = 0.2670) nor an interaction between sex and age (estimate = -0.0318, SE = 0.0293). Probability

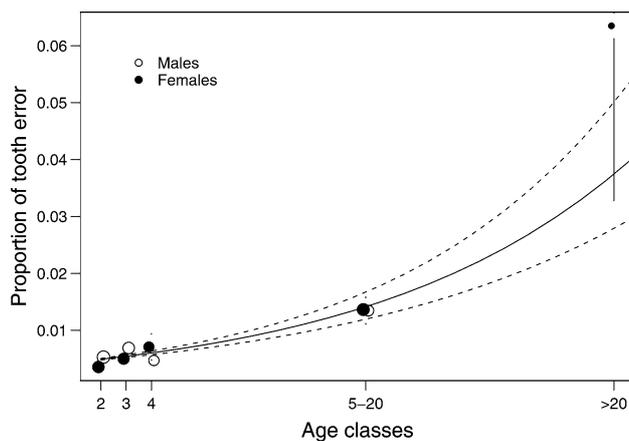


Fig. 1 The proportion of individuals with tooth error by increasing age in red deer. Since there is no sex effect, the predicted model is the same for males and females. The area of data points is proportional to sample size. Note that we have no males in the oldest age group (older than 20 years). For the young age classes, standard errors are so small that they are covered by the data points. The y-axis in females was cut for clarity (i.e., the upper part of the standard error bar of > 20-year-old females was cut, but is similar to the lower part)

for tooth anomalies did vary in space (populations P3 [estimate = -0.6974, SE = 0.1935] and P5 [estimate = -1.033, SE = 0.317] have lower probability of malocclusion than the reference population P1). There was no significant temporal trend in tooth anomalies occurrence over the course of the study (estimate = -0.0091, SE = 0.0083).

As reported earlier, the NAO positively affected body weight of red deer when the index is above -2 (reversed below this level; see Myrsetrud et al. 2001b), and the effect is strongest for positive NAO values (slightly non-linear). Further, novel to this study, the effect of the NAO was stronger in female deer with malocclusion (Fig. 2; Tables 2 and 3; see electronic appendix S1 for the full set of models). Females with malocclusion were on average 4 kg lighter than 'normal' females during harsh climate (NAO around -1) while the weight did not differ when climate was favorable (NAO around 4; Fig. 2; all other factors, also skeletal size, accounted for). The effect of malocclusion was not stronger at high densities (the interaction term density \times malocclusion was not selected in the best models; Table 2). In males, there was no clear effect of malocclusion on body condition, although the pattern was qualitatively consistent with the pattern in females (i.e., the parameter estimates for the mean effect were similar, but the SE was larger; see electronic appendix S2).

Discussion

Our study reports for the first time consequences of malocclusion on body condition, which is a key life history trait in ungulates. Malocclusion was rare (0.6%),

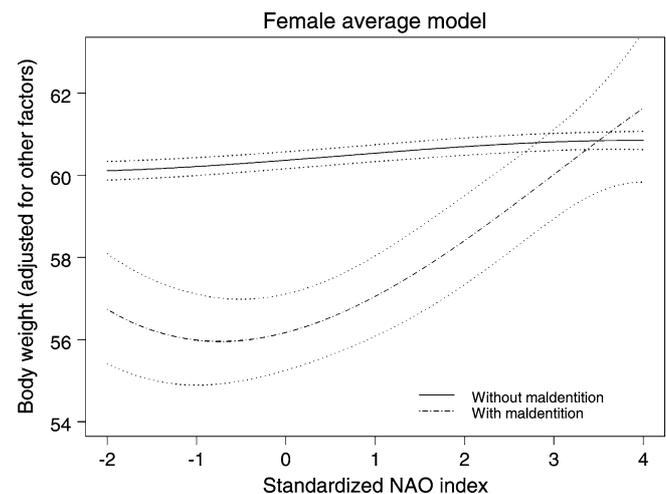


Fig. 2 Influence of climate (as given by winter NAO) on body weight of female red deer with and without malocclusion, adjusted for all other factors (including jaw length, which is a measure of skeletal body size). Climate is most adverse around NAO values close to -2 (see Myrsetrud et al. 2001b for the relationship between NAO and local climate parameters). The (back-transformed logarithmic) predicted values obtained with the parameters from the average model (see Materials and methods) were used to draw the figure

Table 2 The five best models for $\ln(\text{body weight})$ in female Norwegian red deer (see electronic appendix S1 for all models)

Model females	AIC	Δ AIC	w_i
$\ln(\text{body weight}) \sim \ln(\text{jaw length}) + \text{age} + \text{density} + \text{diversity of aspects} + \text{date of culling} + \text{distance to coast} + \text{population} + \text{malodentition}$ + NAO + NAO ² + NAO ³ + NAO \times malodentition + NAO ² \times malodentition + NAO ³ \times malodentition + age \times density	-13958.38	0	0.393
$\ln(\text{body weight}) \sim \ln(\text{jaw length}) + \text{age} + \text{density} + \text{diversity of aspects} + \text{date of culling} + \text{distance to coast} + \text{population} + \text{malodentition}$ + NAO + NAO ² + NAO ³ + NAO \times malodentition + NAO ² \times malodentition + NAO ³ \times malodentition + age \times density	-13957.44	0.94	0.246
$\ln(\text{body weight}) \sim \ln(\text{jaw length}) + \text{age} + \text{density} + \text{diversity of aspects} + \text{date of culling} + \text{distance to coast} + \text{population} + \text{malodentition}$ + NAO ² + NAO ³ + NAO \times malodentition + NAO ² \times malodentition + age \times density	-13956.91	1.47	0.189
$\ln(\text{body weight}) \sim \ln(\text{jaw length}) + \text{age} + \text{density} + \text{diversity of aspects} + \text{date of culling} + \text{distance to coast} + \text{population} + \text{malodentition}$ + NAO + NAO ² + NAO ³ + NAO \times malodentition + NAO ² \times malodentition + NAO ³ \times malodentition	-13955.16	3.22	0.079
$\ln(\text{body weight}) \sim \ln(\text{jaw length}) + \text{age} + \text{density} + \text{diversity of aspects} + \text{date of culling} + \text{distance to coast} + \text{population} + \text{malodentition}$ + NAO + NAO ² + NAO ³ + NAO \times malodentition + NAO ² \times malodentition	-13954.18	4.2	0.048

AIC refers to Akaike's Information Criterion (Akaike 1974), Δ AIC is the difference in AIC value between the given and the best model, w_i is the theoretical probability for the given model to be the right one (w_i of all a priori models sum to 1). See [Materials and methods](#) for details. Terms related to malodentition and the interaction between malodentition and NAO are *bolded*

but had a profound negative effect on body weight in females when the climate was unfavorable.

Too few studies have been reporting population frequencies of malodentition to know if it is generally rare among long-lived mammals. The single earlier study reporting the frequency of malodentition in red deer provides a remarkably similar estimate (0.8% males and 0.6% females had abnormal teeth, $n = 1,091$ individuals) for a population on the southern border of the distribution range (in Spain; Azorit et al. 2002). In roe deer, the frequency of numerical tooth anomalies was much higher (4.85%; $n = 16,510$ upper jaws and 16,177 lower jaws) but did not vary among 14 districts within Czechoslovakia (Zima 1988). Deviations from a normal set of teeth are known to be relatively common in this species (Zima 1988), suggesting that the frequency of malodentition within ungulates is highly species specific.

We find that malodentition occurs more than ten times more often in old than in young females, indicating an accumulation throughout life (see Kratochvil 1984 for a similar pattern in roe deer). The predicted value is much lower than the observed value for the oldest age group (Fig. 1), indicating a rapidly accelerating deterioration of the teeth as the individuals reach their terminal age. This is in line with the observed pattern of reproductive (Langvatn et al. 2004) and phenotypic (Myserud et al. 2001c) senescence in this population. It is likely a strong selection for a set of teeth that lasts for a normal lifetime, but not much longer. However, tooth anomalies are not the main factor causing senescence in this population since it occurs in $< 10\%$ of females that are close to terminal age. Since the frequency of tooth anomalies increased by age, the population frequency of malodentition will rely heavily on the age structure. Norwegian red deer are harvested extensively and age structure is biased towards young individuals, especially in males (Langvatn and Loison 1999).

The rarity of malodentition, especially in young individuals, may be due to strong selection against innate tooth anomalies (some likely genetic in origin). We here demonstrate that such a selection pressure is more severe during unfavorable environmental conditions. In a broader context, this implies that individuals either born with or with a genetic susceptibility to acquire even minor anomalies are punished by external factors to a higher extent than 'normal' individuals under unfavorable conditions. The rarity of the phenomenon implies that malodentition per se is of little importance in population dynamics, especially in harvested populations with a high proportion of younger individuals.

The declining function of teeth by age has a central role in the discussion of proximate factors for senescence in ungulates (Klein and Olson 1960; Gaillard et al. 1993; Loe et al. 2003). Garrott et al. (2002) linked severe malformation of teeth to shorter lifespan in elk. In Loe et al. (2003), we found no relationship between molar height (a proxy for tooth wear) and body condition. Here, we demonstrate that in the same populations,

Table 3 Parameter estimates (including 95% CI) of the average model (see [Materials and methods](#)) for body weight in female red deer

Age categories are 1 2 years old, 2 3 years; 3 4 years, 4 5–20 years (prime age), 5 more than 20 years old (senescent). The effects of age categories 1–4 are shown by contrasting them with age category 5. The same approach is taken on the effect of population (P1 to P5). Parameter estimates with 95%CI not overlapping with 0 are significant on $P < 0.05$ level. Terms related to maldentition and the interaction between maldentition and NAO are bolded

	Parameter estimate	95% CI
Intercept	−8.185495393	−8.84, −7.53
ln(jaw length)	2.01	1.92, 2.09
Age category (1–5)	−0.0367	−0.0736, 0.000231
Age category (2–5)	0.0165	0.00241, 0.0307
Age category (3–5)	0.013	0.00470, 0.0213
Age category (4–5)	0.0095	0.00514, 0.0139
Density	−0.035	−0.0522, −0.0178
Diversity of aspects	0.501	0.254, 0.749
Date of culling	−0.000393	−0.000495, −0.000292
Distance to coast	0.0375	0.0316, 0.0434
Population (P1–P5)	0.0195	0.0163, 0.0228
Population (P2–P5)	0.0164	0.0143, 0.0185
Population (P3–P5)	−0.00634	−0.0138, 0.00113
Population (P4–P5)	−0.0059	−0.00839, −0.00340
Maldentition	−0.072	−0.105, −0.0395
NAO	0.00278	0.000554, 0.00501
NAO ²	0.000154	−0.000278, 0.000586
NAO ³	−8.80E-05	−0.000252, 7.61E-05
Maldentition×NAO	0.00735	−0.0145, 0.0292
Maldentition×NAO²	0.00599	0.00170, 0.0103
Maldentition×NAO³	−0.00063	−0.00226, 0.00100
Age category 1×density	0.0194	−0.0205, 0.0592
Age category 2×density	−0.0111	−0.0267, 0.00446
Age category 3×density	−0.00705	−0.0163, 0.00220
Age category 4×density	−0.00297	−0.00773, 0.00178

maldentition, which decreases tooth function to a higher extent than normal wear, has a strong effect on condition for the females that are affected.

Male body condition was not affected by tooth anomalies to the same extent as females (electronic appendix S2). For each sampled individual, tooth anomalies became effective at an unknown time between the eruption of the permanent teeth (1–2 years of age dependent on the tooth; Loe et al. 2004) and age at harvest. Due to sex-biased harvest (Langvatn and Loison 1999), sampled males with tooth anomalies were younger (mean = 4.41, median = 3 years old) than females (mean = 9.58, median = 8 years old). If there had been a cumulative effect of tooth anomalies, the lacking condition effect in males could be because they (on average) have been subjected to maldentition for a shorter time period than females. However, we could not detect such a cumulative effect in our analyses (the interaction term age × maldentition was not selected in the best models). Maldentition may also interact with or speed up the rate of tooth wear, which may potentially come into play for the older females, although we did not find a body condition effect of normal wear in Loe et al. (2003). In general, body weights of males (CV = 24%) are much more variable than those of females (CV = 15%), which may mask a minor effect of maldentition in males. To detect a significant effect of tooth anomalies on body weight would therefore require a larger data set for males than for females (they are now of similar size; Table 1), implying that the male data set may be marginal. Indeed, as the parameter estimates for the mean effect were similar for males and females (but the SE was larger for males), lower power for males may likely be the case.

The effect of tooth anomalies on female body condition was dependent on climate, but not on population density. Adverse climate and population density are two forms of environmental stress that are known to affect herbivore performance. During winter, red deer prefer blueberry and cowberry in the field layer and only shift to browse in the tree layer if the former is not available (Ahlén 1965, 1975). Therefore, severe climate and high density would intuitively lead to the same effect, namely a shift towards rougher type of diets due to, respectively, snow coverage and reduction of easily chewable forage in the field layer. We identified an overall negative effect of population density (i.e., a main effect) in agreement with earlier work (e.g., Mysterud et al. 2001b), but no interaction between maldentition and density was detected. A likely explanation for why female deer with maldentition are more susceptible to unfavorable climate than to high density is that deer habitats per date are not grazed to such an extent that would cause a sufficiently large shift in diet types. Along the west coast of Norway, winters with much snow at high altitudes (summer range) coincide with less snow at low altitudes (winter range) (Mysterud et al. 2000). The NAO is known to at least partly operate through summer foraging conditions, as it affects snow accumulation and hence plant phenology and foraging conditions during early summer at high altitudes (Mysterud et al. 2001b). If snow cover totally inhibits access to the field layer, this would force deer to eat a lower quality diet and make tooth anomalies fatal. As it is more difficult to see how maldentitions can affect performance from the summer grazing situation, our study therefore also provides some indirect evidence that the NAO may also operate through winter conditions.

Acknowledgements We gratefully acknowledge the financial support provided by the AURORA grant from the Research Council of Norway (NFR) and EGIDE (French Ministry for Foreign Affairs) to L.E.L and C.B. We thank David Firth, Nigel G. Yoccoz, Torbjørn Ergon, and Jon Olav Vik for valuable statistical advice, and Jean-Michel Gaillard and the two anonymous referees for valuable comments on an earlier draft. We declare that no action associated with this work violates the current laws of Norway.

References

- Agresti A (1990) Categorical data analysis. Wiley, New York
- Ahlén I (1965) Studies on the red deer, *Cervus elaphus* L., in Scandinavia. Swed Wildl Res 3:177–376
- Ahlén I (1975) Winter habitats of moose and deer in relation to land use in Scandinavia. Swed Wildl Res 9:45–192
- Akaike H (1974) A new look at statistical model identification. IEEE T Automat Contr AU 19:716–722
- Azorit C, Munõs-Cobo J, Analla M (2002) Abnormal teeth in the Spanish red deer. Z Jagdwiss 48:252–260
- Buckland ST, Burnham KP, Augustin NH (1997) Model selection: an integral part of inference. Biometrics 53:603–618
- Burnham KP, Anderson DR (1998) Model selection and inference: a practical information-theoretic approach. Springer, Berlin Heidelberg New York
- Conner MM, White GC, Freddy DJ (2001) Elk movement in response to early-season hunting in northwest Colorado. J Wildl Manage 65:926–940
- Coulson T, Milner-Gulland EJ, Clutton-Brock T (2000) The relative roles of density and climatic variation on population dynamics and fecundity rates in three contrasting ungulate species. Proc R Soc Lond Ser B 267:1771–1779
- Efron B, Tibshirani RJ (1993) An introduction to the bootstrap. Chapman and Hall, London
- Ericsson G, Wallin K (2001) Age-specific moose (*Alces alces*) mortality in a predator-free environment: Evidence for senescence in females. Ecoscience 8:157–163
- Firth D (1993) Bias reduction of maximum likelihood estimates. Biometrika 80:27–38
- Gaillard J-M, Delorme D, Boutin J-M, Van Laere G, Pradel R (1993) Roe deer survival patterns: a comparative analysis of contrasting populations. J Anim Ecol 62:778–791
- Garrott RA, Eberhardt LL, Otton JK, White PJ, Chaffee MA (2002) A geochemical trophic cascade in Yellowstone's geothermal environments. Ecosystems 5:659–666
- Gordon IJ, Illius AW (1988) Incisor arcade structure and diet selection in ruminants. Funct Ecol 2:15–22
- Hallett TB, Coulson T, Pilkington JG, Clutton-Brock TH, Pemberton JM, Grenfell BT (2004) Why large-scale climate indices seem to predict ecological processes better than local weather. Nature 430:71–75
- Heinze G, Schemper M (2002) A solution to the problem of separation in logistic regression. Stat Med 21:2409–2419
- Hurrell JW, Van Loon H (1997) Decadal variations in climate associated with the North Atlantic Oscillation. Clim Change 36:310–326
- Johnson JB, Omland KS (2004) Model selection in ecology and evolution. Trends Ecol Evol 19:101–108
- Kierdorf U, Kierdorf H (2002) Supernumerary incisiform tooth in a red deer. Z Jagdwiss 48:276–280
- King G, Zeng L (2001) Explaining rare events in international relations. Int Organ 55:693–715
- Klein DR, Olson ST (1960) Natural mortality pattern of deer in southeast Alaska. J Wildl Manage 24:80–88
- Kratochvil Z (1984) Veranderingen am Gebiss des Rehwildes (*Capreolus capreolus* L.). Folia Zool 83:209–222
- Langvatn R (1977) Criteria of physical condition, growth and development in Cervidae,—suitable for routine studies. Nordic Council for Wildlife Research, Stockholm
- Langvatn R, Loison A (1999) Consequences of harvest on age structure, sex ratio and population dynamics of red deer in central Norway. Wildl Biol 5:213–223
- Langvatn R, Albon SD, Burkey T, Clutton-Brock TH (1996) Climate, plant phenology and variation in age at first reproduction in a temperate herbivore. J Anim Ecol 65:653–670
- Langvatn R, Mysterud A, Stenseth NC, Yoccoz NG (2004) Timing and synchrony of ovulation in red deer constrained by short northern summers. Am Nat 163:763–772
- Loe LE, Mysterud A, Langvatn R, Stenseth NC (2003) Decelerating and sex-dependent tooth wear in Norwegian red deer. Oecologia 135:346–353
- Loe LE, Meisingset E, Mysterud A, Langvatn R, Stenseth NC (2004) Phenotypic and environmental correlates of tooth eruption in red deer (*Cervus elaphus*). J Zool 262:83–89
- McCullagh P, Nelder JA (1989) Generalized linear models. Chapman and Hall, London
- Mitchell B (1967) Growth layers in dental cement for determining the age of red deer (*Cervus elaphus* L.). J Anim Ecol 36:279–293
- Mysterud A, Yoccoz NG, Stenseth NC, Langvatn R (2000) Relationships between sex ratio, climate and density in red deer: the importance of spatial scale. J Anim Ecol 69:959–974
- Mysterud A, Langvatn R, Yoccoz NG, Stenseth NC (2001a) Plant phenology, migration and geographic variation in body weight of a large herbivore: the effect of a variable topography. J Anim Ecol 70:915–923
- Mysterud A, Stenseth NC, Yoccoz NG, Langvatn R, Steinheim G (2001b) Nonlinear effects of large-scale climatic variability on wild and domestic herbivores. Nature 410:1096–1099
- Mysterud A, Yoccoz NG, Stenseth NC, Langvatn R (2001c) The effects of age, sex and density on body weight of Norwegian red deer: evidence of density-dependent senescence. Proc R Soc Lond Ser B 268:911–919
- Pérez-Barberia FJ, Gordon IJ (1998) Factors affecting food comminution during chewing in ruminants: a review. Biol J Linn Soc 63:233–256
- R Development Core Team (2004) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria
- Reimers E, Nordby Ø (1968) Relationships between age and tooth cementum layers in Norwegian reindeer. J Wildl Manage 32:957–961
- Skogland T (1988) Tooth wear by food limitation and its life history consequences in wild reindeer. Oikos 51:238–242
- Venables WN, Ripley BD (1999) Modern Applied Statistics with S-plus. Springer, Berlin Heidelberg New York
- Yoccoz NG, Mysterud A, Langvatn R, Stenseth NC (2002) Density-dependent and age related reproductive effort in male red deer. Proc R Soc Lond Ser B 269:1523–1528
- Zima J (1988) Incidence of dental anomalies in *Capreolus capreolus* from Czechoslovakia. Folia Zool 37:129–144