

Effects of age, sex and density on body weight of Norwegian red deer: evidence of density-dependent senescence

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There are only a few recent studies that have demonstrated senescence in ungulates and nothing is known regarding how patterns of senescence may vary as a function of density. Senescence in general is linked to the cost of reproduction, which probably increases with density in ungulates and may differ between the sexes. Further, senescence in ungulates is also regarded to be a function of tooth wear rates. As density dependence and sexual differences in food choice have been well documented, this may lead to different tooth wear rates and, thus, possibly density-dependent and sex-specific patterns of senescence. We therefore investigated the effects of age, sex, density and their possible interactions on the variability of body weight in 29 047 red deer harvested during 1965–1998 from Norway, out of which 380 males and 1452 females were eight years or older. There was clear evidence that spatio-temporal variation in density correlated negatively with body weights. In addition, there was evidence of senescence in both male and female red deer. Age at onset of senescence in females was after 20 years of age and independent of population density. In males, the onset and rate of senescence increased with increasing population density. The onset of senescence for males was at *ca.* 12 years of age at low density, but decreased to approximately ten years of age at high density. The pattern of density-dependent senescence in males, but not that in females, can be explained if (i) the cost of reproduction increases with density more strongly in male than in female red deer, and/or (ii) tooth wear rates are density dependent in males, but not in females. We discuss the ability of these two different, not mutually exclusive hypotheses in explaining the observed pattern of senescence.

Keywords: *Cervus elaphus*; cost of reproduction; density dependence; tooth wear; ungulates

1. INTRODUCTION

The progressive loss of function accompanied by decreased survival and reproductive rate with increasing age, which is termed senescence, may be explained in an evolutionary context by the antagonistic pleiotropy hypothesis (Medawar 1946; Williams 1957; Hamilton 1966; Rose 1991), the disposable soma hypothesis (Kirkwood & Austad 2000) or the mutation-accumulation hypothesis (Medawar 1946; Edney & Gill 1968; reviewed in Zwaan 1999). In a non-evolutionary context, the senescence phenomenon may be explained as a by-product of metabolism (Sacher 1978). In natural populations, very few individuals may reach the age at which their ability to survive or reproduce will decrease as a result of senescence (Medawar 1952; Comfort 1979; Loison *et al.* 1999a). The focus of studies on senescence among mammals has therefore usually been to evaluate whether senescence occurs at all (Promislow 1991; Gaillard *et al.* 1994; Sibly *et al.* 1997) and the methodological problems related to demonstrating this (Gaillard *et al.* 1994; Sibly *et al.* 1997). There has been little effort invested in testing specific hypotheses regarding the mechanisms leading to inter- and intraspecific patterns of senescence (Bell 1984; Rose 1985; Loison *et al.* 1999a).

Some ungulates are well suited for studies on senescence, as their age can be accurately estimated on the

basis of tooth cementum layers (Reimers & Nordby 1968) and they are so long lived that senescence cannot be confounded with seasonality as, for example, was the case in studies on rodents (Slade 1995). Loison *et al.* (1999a) recently presented convincing evidence of decreased survival with increasing age in five populations of ungulates and Catchpole *et al.* (2000) found evidence of senescence-related mortality in Soay sheep (*Ovis aries*), while Bérubé *et al.* (1999) demonstrated evidence of reproductive senescence in bighorn sheep (*Ovis canadensis*). Sex differences in survival in ungulates are related to neither sexual dimorphism in body mass or to the level of polygyny, suggesting that differences in the social behaviour of species, particularly mating system and the level of male–male aggression, may be more important than simply the level of polygyny in explaining sexual differences in survival (Loison *et al.* 1999a).

However, the ecological conditions that influence intraspecific patterns of senescence are less well understood. A cost of reproduction, where an increase in reproductive rate reduces future survival or fecundity, might be attributable to pleiotropic gene action that generates senescence (Gustafsson & Pärt 1990; Stearns 1992; Bérubé *et al.* 1999). Gustafsson & Pärt (1990) demonstrated that the clutch size of older individuals in the collared flycatcher (*Ficedula albicollis*) was affected by their reproductive effort early in life, whereas positive phenotypic correlations between early and late reproduction have been reported for some other birds and

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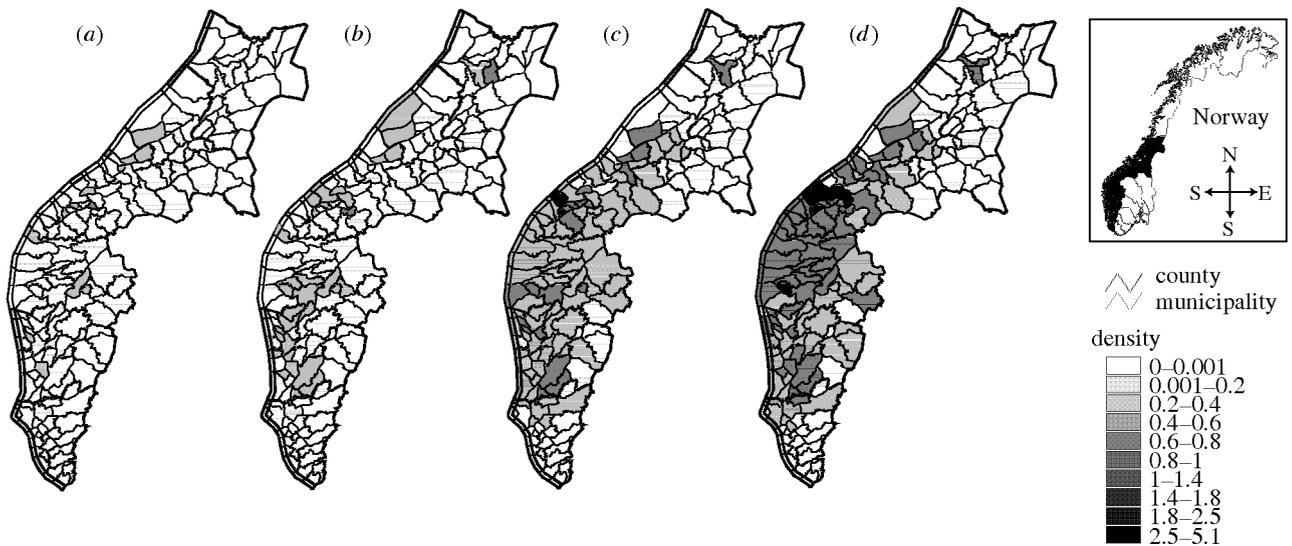


Figure 1. Geographical location of the study area in Norway and the density of red deer calculated as the total harvest of red deer divided by the qualifying area (see §2(a)) in (a) 1965, (b) 1975, (c) 1985 and (d) 1995.

insects (Stearns 1992). Bérubé *et al.* (1999) found a weak, positive relationship between reproductive success up to seven years of age and reproductive success starting at eight years in bighorn sheep. Increasing population density in *Drosophila* generally decreases longevity (reviewed in Graves & Mueller 1993), but no similar data have been presented for mammals. High population density can increase reproductive costs (Bérubé *et al.* 1996, 1999; Festa-Bianchet *et al.* 1998) and one may therefore also expect density-dependent senescence in ungulates. Clutton-Brock *et al.* (1982, p. 76) found that, for red deer (*Cervus elaphus*) on Rum, Scotland, milk hinds had lower fecundity than yields and that this difference increased with population density, i.e. there was a density-dependent cost of reproduction. The major costs of reproduction for ungulate males originate from fighting with other males, not from copulations (Geist 1986; Gosling *et al.* 1987; Festa-Bianchet *et al.* 1990; Alvarez 1993; Komers *et al.* 1994). There may be an increased risk of fighting when densities are high (Alvarez 1993; Pélabon *et al.* 1999), although this is not always the case (Clutton-Brock *et al.* 1982). One might thus expect that the rate of senescence could increase with density in males. Further, senescence in ungulates is regarded to be a function of tooth wear rates (Tyler 1987; Gaillard *et al.* 1993). As density dependence (Fowler 1987; Freeland & Choquenot 1990) and sexual differences (Clutton-Brock *et al.* 1982; Mysterud 2000) in food choice have been well documented, we may expect different tooth wear rates due to sex and density and, thus, possibly density-dependent and sex-specific patterns of senescence.

In ungulates, body size is a major determinant of reproduction in females (Reimers 1983; Gaillard *et al.* 1992, 1998; Langvatn *et al.* 1996; Putman *et al.* 1996; Sæther 1997), competitive ability in males (Clutton-Brock *et al.* 1982) and overwinter survival (White & Bartmann 1998; Loison *et al.* 1999b). Body size therefore has an important influence on the fitness of individuals as well as on population dynamics (Klein 1970; Sæther 1985) and is

thus a well-suited index for estimating senescence in ungulates (Jorgenson *et al.* 1997; Bérubé *et al.* 1999). Comprehensive, individual-based studies of red deer on Rum, Scotland, have demonstrated strong density-dependent effects on several demographic parameters, including body weight (Clutton-Brock *et al.* 1982, 1985, 1987a,b, 1997a; Coulson *et al.* 1997). In order to test for senescence or density dependence in senescence reliably, the importance of density-dependent effects on body weight in general must therefore be assessed. Recently, analysis of variation of body weight in Norwegian red deer has produced contrasting results regarding the effect of density. A second goal was therefore to determine whether or not there was significant density dependence (Post *et al.* 1997; Loison *et al.* 1999b) in this population. We tested for the effects of age, sex, density and their possible interactions on a data set of Norwegian red deer that contains data on 29 047 individuals sampled from 105 municipalities along the western part of Norway between 1965 and 1998. This data set contains data on 380 males and 1452 females of eight years or older.

2. MATERIAL AND METHODS

(a) Study area

The study area was the western part of southern Norway (figure 1), which is the main area for red deer in Norway (Langvatn *et al.* 1996). The data came from 105 municipalities in the counties of Rogaland (6), Hordaland (23), Sogn and Fjordane (22), Møre and Romsdal (30), Sør-Trøndelag (17) and Nord-Trøndelag (7). We hereafter refer to Rogaland and Hordaland as population P1, Sogn and Fjordane as population P2, Møre and Romsdal and Sør-Trøndelag as population P3 and Nord-Trøndelag as population P4 (after Forchhammer *et al.* 1998). The island Hitra (which was not included in Forchhammer *et al.* (1998)) was treated as a separate population (P5), since it is a typical island population with special demographic characteristics (Wegge 1975; Langvatn *et al.* 1996). The vegetation on the west coast of Norway is mostly in the boreone-moral zone (Abrahamsen *et al.* 1977). Exceptions to this general

pattern are a small area around the Hardangerfjorden in Hordaland, which is in the nemoral zone and some areas not far from the Trondheimsfjorden, which are in the southern boreal zone. From Rogaland to Møre and Romsdal forests are dominated by deciduous and pine forest. However, there has been a large-scale programme for planting Norway spruce (*Picea abies*), which is an important winter habitat for red deer (Ahlén 1965). The areas in Sør-Trøndelag up to Trondheimsfjorden are dominated by birch and pine, whereas spruce forest dominates some areas north of this. In general, temperature and precipitation decline from south to north and from the coast to inland, while snow depth increases (Langvatn *et al.* 1996; Mysterud *et al.* 2000). In summer both the length of the growing season and total degree days decline from south-west to north-east. Topography is generally steeper in the inland areas (Langvatn & Albon 1986; Albon & Langvatn 1992).

(b) Red deer data on body weight

Red deer were sampled during the annual autumn harvests of 1965–1998 (see Langvatn *et al.* 1996; Post *et al.* 1997). Hunting is controlled through licences issued by local wildlife boards in each municipality. Red deer may only be shot between 10 September and 15 November, although the actual hunting periods vary slightly between these dates in different counties. In cooperation with the local wildlife boards, hunters provided mandibles from all animals shot, together with records of sex, date, locality (municipality) and body weight. Date of shooting was treated as a continuous variable and quantified as the day on which an animal was recorded as shot, starting with day 1 for 1 September and counting consecutively forward to 31 December, which is numbered as day 122 (Post *et al.* 1997). Body weight is dressed weight, i.e. live weight minus head, skin, viscera, bleedable blood and metapodials (Langvatn 1977). Dressed weight in hinds is *ca.* 58% of live weight. Age determination in calves and yearlings was based on tooth eruption patterns, whereas older animals were aged using annuli in the cementum of the first incisor (Reimers & Nordby 1968). This technique was found to be highly reliable for Norwegian red deer when conducting blind tests including a large number of marked animals of known age (R. Langvatn, unpublished data). The maximum recorded longevity among the red deer used in the analysis was 19 years for males and 26 years for females, although our data file contains one male aged 22 years for which body weight was not known.

Some of these data have been used in previous analyses with regard to temporal variation in body weights (Langvatn *et al.* 1996; Post *et al.* 1997) along with data on 469 deer from 1978 and 1983 for geographical variation (distance from the coast and latitude) (Langvatn & Albon 1986). However, these earlier analyses used a rather coarse geographical scale (six main regions) (Langvatn & Albon 1986; Langvatn *et al.* 1996; Post *et al.* 1997) and we have recently demonstrated that density dependence in this population is more reliably estimated at a local (municipality) spatial scale (Mysterud *et al.* 2000). The choice of spatial scale may be particularly important for analysis of this data set on body weights, as some municipalities had been sampled regularly while others had only been sampled infrequently or just once and, thus, there was an imbalanced spatio-temporal sampling design. By pooling data in six main regions (Langvatn & Albon 1986; Post *et al.* 1997) much information is lost and, more importantly, since the data did not come from the same municipalities each year, the use of linear models may have produced biased results. In addition, Post *et al.* (1997)

used linear models and a log transformation of age for calculating their yearly ‘idealized’ red deer, which did not take into account the fact that weight may possibly not increase after prime age is reached or may even decline due to senescence.

(c) Red deer hunting data: an index for density

In order to obtain an index for density that reflected both spatial and temporal components of density, we divided the total number of red deer harvested each year by the so-called ‘qualifying area’ in each municipality (the area reported for 1997 was used for all years) (Statistics Norway 1977–1998). The qualifying area is the area of suitable red deer habitat within each municipality constituting the basis for harvest quotas as approved by the management authorities.

Most cervid populations in Scandinavia have increased fairly steadily over the last few decades, e.g. moose *Alces alces* (Cederlund & Markgren 1987), red deer (Forchhammer *et al.* 1998) and roe deer *Capreolus capreolus* (Andersen *et al.* 1998). It has therefore been debated whether entering year (as a continuous variable) (Hjeljord & Histøl 1999; Loison *et al.* 1999*b*), total harvest at a coarse scale (Post *et al.* 1997) or total harvest at a local scale divided by qualifying area (Mysterud *et al.* 2000) is the best index for density in these populations. The problem of using total harvest as an index for density in harvested populations arises from the fact that there is usually a time-lag between increased or decreased density and increased or decreased harvest quotas (Fryxell *et al.* 1988, 1991; Solberg *et al.* 1999). The problem of entering year as a continuous variable as an index for density is that a population increase over time is often not linear and that population increases may be very different between different municipalities (spatial density component). Although changes in harvest from one year to the next may say little about an increase or decrease in abundance (Solberg *et al.* 1999), the increased harvest certainly reflects changes in population size over a time-span of five or ten years, as long as we use the absolute harvest number when calculating density (Mysterud *et al.* 2000) and not the year to year changes in abundance used when detrending these time-series (as done by Post & Stenseth 1999). Density also has a strong spatial component and the spatio-temporal variation in density can thus be estimated best by using the total harvest (from a specific year) to qualifying area (from 1997) in each municipality (Mysterud *et al.* 2000).

(d) Statistical analyses

We used a combination of general linear models (GLMs) and general additive models (GAMs) (Hastie & Tibshirani 1990) for analysing variation in body weight. A logarithmic transformation ($\ln(\text{weight})$) of body weight was sufficient for obtaining residuals with constant variance when using GLMs. However, as the relationship between age and $\ln(\text{weight})$ was nonlinear (see below), we used GAMs for assessing the robustness of the results with regard to misspecification of the systematic part of the model. As the GAMs provided the same results as the GLMs, we only present results obtained using the latter models, mainly because the coefficients of linear models are easily comparable between studies and because interactions can easily be tested for. However, we used GAMs for graphically describing the relationship between body weight and age in females and males at both high and low density. We restricted our GLMs to animals of eight years or older, since any evidence of senescence is not expected prior to this age (e.g. Clutton-Brock *et al.* 1982; Gaillard *et al.* 1993; Loison *et al.* 1999*a*). This assumption was also supported by the GAMs (see § 3).

Table 1. *Parameter estimates (obtained from the general linear model, i.e. least-squares estimates and from 2000 parametric bootstrap replicates) with bootstrapped standard errors and confidence intervals*

(The reference level for the factor sex is 'female' and that for population is 'P1'. Other parameters are given as the differences between levels.)

parameter	least-squares estimate	bootstrap estimate	bootstrap s.e.	95% CI
intercept	6.42	6.42	0.014	6.39 to 6.44
sex (M-F)	0.63	0.63	0.030	0.58 to 0.69
age ₁₂	-0.0079	-0.0079	0.0033	-0.014 to -0.0013
age ₁₂ ²	-0.00059	-0.00059	0.00023	-0.0011 to -0.00016
density	-0.060	-0.060	0.013	-0.084 to -0.034
density × age ₈	0.0034	0.0034	0.0028	-0.0018 to 0.0093
population (P2-P1)	0.045	0.046	0.010	0.024 to 0.065
population (P3-P1)	0.099	0.099	0.0093	0.081 to 0.118
population (P4-P1)	0.083	0.083	0.028	0.023 to 0.134
population (P5-P1)	-0.076	-0.076	0.014	-0.102 to -0.047
age ₁₂ × population (P2-P1)	0.0064	0.0066	0.0027	0.0011 to 0.012
age ₁₂ × population (P3-P1)	0.0088	0.0089	0.0026	0.0039 to 0.014
age ₁₂ × population (P4-P1)	0.013	0.013	0.0082	-0.0034 to 0.029
age ₁₂ × population (P5-P1)	0.012	0.012	0.0030	0.0064 to 0.018
age ₁₂ × sex (M-F)	-0.0025	-0.0025	0.0085	-0.041 to -0.007
age ₁₂ ² × sex (M-F)	-0.0025	-0.0025	0.0011	-0.0047 to -0.0002
density × age ₈ × sex (M-F)	-0.023	-0.023	0.0068	-0.037 to -0.010
date of culling	-0.00029	-0.00029	0.00017	-0.00062 to 0.000036
date of culling × sex (M-F)	-0.0029	-0.0029	0.00061	-0.0040 to -0.0017
date of culling × age ₁₂	0.000024	0.000024	0.000046	-0.000070 to 0.00011
date of culling × age ₁₂ × sex (M-F)	0.00046	0.00046	0.00019	0.00006 to 0.00083
NAO	0.0026	0.0026	0.0014	-0.0001 to 0.0051
proportion of high altitude habitat	-0.206	-0.206	0.044	-0.290 to -0.117
distance from the coast	0.105	0.105	0.015	0.075 to 0.133

The relationship between age and ln(weight) in the GLMs using animals of eight years or older was adequately described using a second-order polynomial of age (see also Loison *et al.* 1999a). This means that the decrease in ln(weight) with age was accelerating with age at a constant rate. In order to provide readily interpretable coefficients, we used age minus 12 (hereafter denoted by age₁₂) in the GLM as a polynomial term (see e.g. Cox & Snell 1981). The coefficient for age₁₂ then represented the rate of decrease of ln(weight) for animals aged 12 years and the coefficient for age₁₂² was the curvature at this age (i.e. the acceleration in the decrease). We scaled the age variable at 12 years as it proved convenient for obtaining readily interpretable parameters regarding senescence, while using older ages was not possible due to limitations set by the sample size. Using age₁₂ also resulted in a lower sampling correlation between coefficients. Other covariates such as the North Atlantic Oscillation (NAO) index (Post *et al.* 1997; Post & Stenseth 1999), date of culling (Post *et al.* 1997), distance from the coast (Langvatn & Albon 1986) and proportion of high-altitude habitat (A. Mysterud, R. Langvatn, N. G. Yoccoz and N. C. Stenseth, unpublished data) were included in the model in order to correct for bias due to the imbalance in the study design. If the fitted model is too complex, this would result in estimates with lower bias but lower precision and bias is a more important issue in observational studies (e.g. Cochran & Rubin 1973). We therefore used a model including terms which may not be significant, but which could influence the estimates for the coefficients of interest (the relationship of ln(weight) and age). In particular, because of the recent changes in population densities of red deer in Norway (Forchhammer *et al.* 1998), we could expect a large

spatial heterogeneity and, thus, the spatial covariates were included in order to correct for such heterogeneity.

In order to assess the interaction between density and age, we restricted the analysis to a multiplicative term between density and age minus 8 years (denoted hereafter as density × age₈). This term represented the increase in the rate of decrease of ln(weight) with density for individuals older than eight years. We also investigated if there was any evidence for higher order effects by using the terms density × age₈² and density² × age₈.

We assessed the quality of the fit of a given model by using non-parametric models (lowess regression) fitted on residuals. Parametric bootstrapping (Efron & Tibshirani 1993) was used for calculating confidence intervals (CIs) for parameter estimates. A total of 2000 bootstrap samples were used.

3. RESULTS

The GLM that included the effects of sex, density, population, age₈, age₁₂² and date of culling, and the interactions density × age₈, sex × age₁₂, sex × age₁₂², sex × density × age₈, age₁₂ × population, date of culling × sex, date of culling × age₁₂ and date of culling × sex × age₁₂ as well as the covariates NAO, distance from the coast and proportion of high-altitude habitat was used for further inference (see table 1). The *R*² of this model was high (0.709) given that 1832 individuals were used. Residual plots indicated some residual systematic variation of ln(weight) with age, but fitting a higher-order polynomial (up to sixth order) in order to remove this systematic variation did not change the estimates for the other

parameters of the model (see below). We therefore mainly present the results of the simpler model.

Male red deer were larger than female red deer (table 1). There was an overall large negative effect of local (municipality) density on $\ln(\text{weight})$. This result was also robust when using the total harvest in Norway as an index for density as used earlier by Post *et al.* (1997), when entering year as a continuous variable as an index for density (i.e. body weights decreased over time) as used by Loison *et al.* (1999b) and when splitting the analysis into spatial (i.e. considering density variation between municipalities within a year) and temporal (i.e. considering density variation within a municipality over time) density components separately. The effect of density was approximately linear for females (figure 2a), although the curve was very slightly concave when tested in a GAM model (d.f._{splines} = 1 versus 2, $F = 84.444$ and $p < 0.001$), whereas the curve for males was more convex (figure 2b) (d.f._{splines} = 3 versus 4, $F = 4.000$ and $p = 0.046$). There was evidence of senescence in both male and female red deer. Based on interpretation of the GAM plots, age at onset of senescence in females was after 20 years of age and independent of population density (figure 3a). In males, the onset and rate of senescence increased with increasing population density. The onset of senescence for males was at *ca.* 12 years of age at low density, but decreased to approximately ten years of age at high density (figure 3b). We used as many degrees of freedom as necessary in the GAM in order to include all significant terms (females, d.f._{splines} = 7 versus 8, $F = 3.874$ and $p = 0.044$, and males, d.f._{splines} = 5 versus 6, $F = 5.432$ and $p = 0.020$). The GLM gave similar results. There was no interaction between density and age₈ in females, but there was a negative interaction in males, i.e. there was evidence of an increased rate of senescence in males but not in females, with increasing density (the third-order interaction density \times age₈ \times sex was highly significant) (d.f. = 1808, $t = 3.430$ and $p = 0.001$). At low population density (i.e. when density \times age₈ = 0), there was no apparent decrease in $\ln(\text{weight})$ for females and males with age, except in population PI and the curvature was very weak (i.e. the increase in the rate of senescence was very weak). There was no evidence for a difference in the rate or curvature (i.e. no acceleration of rate) of the $\ln(\text{weight})$ to age curve between males and females after density effects had been taken into account. There were large geographical effects on $\ln(\text{weight})$, both between populations and as a function of the geographical covariates distance from the coast and proportion of high-altitude habitat. The weight of males, but not females, decreased with date of culling and this effect decreased with age. There was no evidence for an effect of the NAO for these old individuals. There was no evidence of interactions between population and other variables (table 1).

These results were not dependent on including more complex relationships between age and $\ln(\text{weight})$. A sixth-order polynomial for age (including an interaction between age and sex) resulted in an estimated coefficient for the interaction between age, density and sex equal to -0.0270 (s.e. = 0.0069) as compared with the previous estimate of -0.0234 (s.e. = 0.0068). Similarly, including higher terms for the interaction between density and age did not change the results in a significant way.

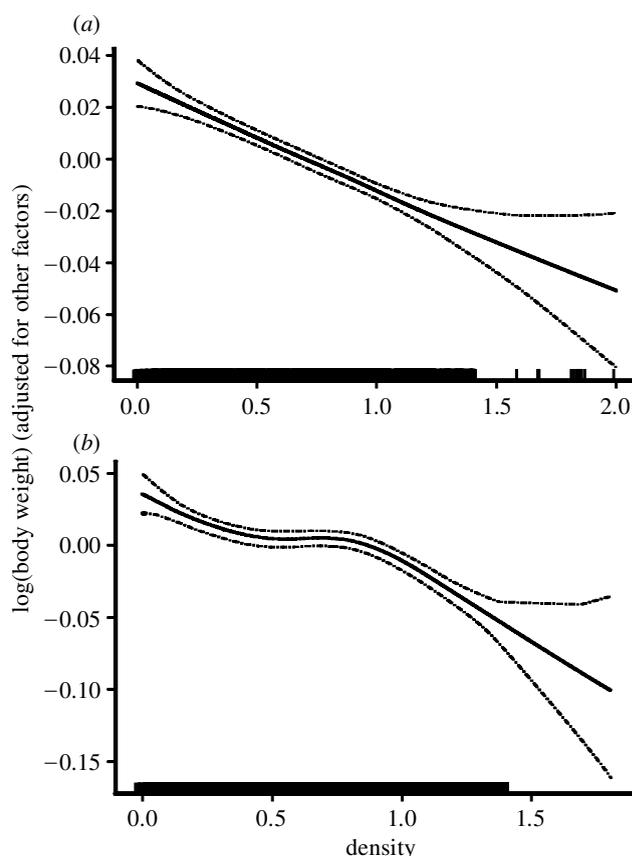


Figure 2. The relationship between body mass and density in adult (more than one-year-old) Norwegian red deer presented as a result of fitting an additive model to the red deer data on body weights with smooth functions on a continuous predictor (with d.f._{splines} = 2 for density in females and d.f._{splines} = 4 for for density in males). The dashed lines are 95% pointwise confidence intervals. The tick marks show the locations of the observations on that variable (see Venables & Ripley 1994). We used annual culling divided by the qualifying area as an index for density (see § 3). (a) Females and (b) males.

4. DISCUSSION

(a) Senescence

The relationship between demographic traits and age in ungulates can usually be fairly well described by the Caughley (1966)-like model, i.e. a three-stage model with a relatively stable period termed prime age with lower survival, reproduction and body weight below and above this prime age (Gaillard *et al.* 1993, 1998; Loison *et al.* 1999a). This was also the case for the Norwegian red deer and our analyses revealed clear evidence of senescence in both males and females (figure 3). Senescence in body weight has previously been demonstrated in ungulates based on longitudinal data in bighorn sheep (Jorgenson *et al.* 1997; Bérubé *et al.* 1999), while we used transversal data for red deer. In the Norwegian red deer, age at onset of senescence in females was after 20 years of age, while that of males was only 10 to 12 years (dependent on population density; see below). Bérubé *et al.* (1999) demonstrated that the onset of senescence-related mass loss occurred three years prior to reproductive senescence, but three years after the onset of survival senescence

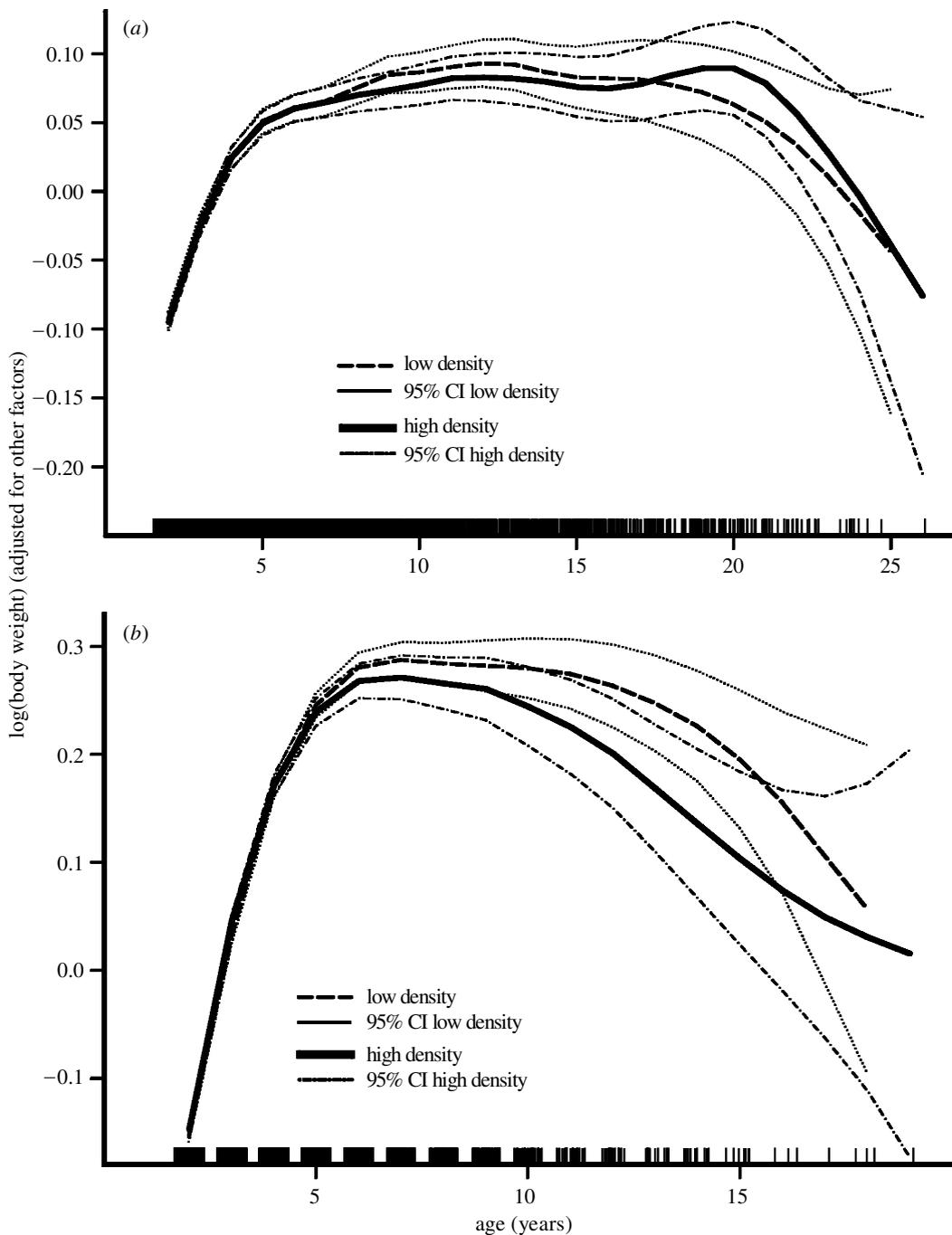


Figure 3. The relationship between body mass and age in adult (more than one-year-old) Norwegian red deer presented as a result of fitting an additive model to the red deer data on body weights with smooth functions on a continuous predictor (with $d.f_{\text{splines}} = 8$ for age in females and $d.f_{\text{splines}} = 6$ for age in males). The tick marks show the locations of the observations on that variable (see Venables & Ripley 1994). (a) Females and (b) males.

(Jorgenson *et al.* 1997). Senescence in survival, reproduction and body weight is thus not directly correlated.

We found clear evidence of a density-dependent rate of senescence in males (figure 3*b*), but not in females (figure 3*a*). These sex-specific, density-dependent rates of senescence can possibly be explained in terms of (i) sex-specific costs of reproduction, and/or (ii) sex-specific tooth wear rates with increasing density.

- (i) The cost of reproduction is generally regarded as the kind of pleiotropic gene action that generates senescence (Gustafsson & Pärt 1990; Stearns 1992).

Although evidence of increased costs of reproduction has been presented for female red deer (Clutton-Brock *et al.* 1982, p. 76), there was no evidence that the rate of senescence increases with increasing density for hinds (figure 3*a*). It is possible that males experience increased costs of reproduction more sharply as density increases due to intermale aggression. Strong density dependence in the cost of reproduction has been demonstrated in non-lekking populations of fallow deer (*Dama dama*) (Alvarez 1993; Pélabon *et al.* 1999). However, although harem size increased with population density, the relative

frequency of fights among red deer stags was lower at high density (Clutton-Brock *et al.* 1982, p. 274; see also Clutton-Brock *et al.* 1997*b*). However, we cannot exclude the possibility that the cost of reproduction in males measured as frequency of fights (Clutton-Brock *et al.* 1982) could be negatively correlated with some mortality cost of reproduction. As our data is transversal, the density-dependent senescence observed in males may be due to an increased mortality cost of reproduction with increasing density for the largest males only (i.e. selection). High population density is commonly associated with increased mortality of males relative to females (Clutton-Brock *et al.* 1997*b*) and this cost of reproduction may affect the most successful (and largest) males most strongly (Gibson & Guinness 1980).

- (ii) It has been suggested that increased tooth wear in old age may lower feeding efficiency and, thus, be responsible for senescence in ungulates (Tyler 1987; Gaillard *et al.* 1993). The observed sexual differences in diet and habitat use observed for red deer and other sexually dimorphic ungulates (e.g. Clutton-Brock *et al.* 1982, 1987*c*; Illius & Gordon 1987; Mysterud 2000) may lead to faster tooth wear rates in males than in females (Van Deelen *et al.* 2000). Further, as density increases, ungulates often eat a lower quality diet (Fowler 1987; Freeland & Choquenot 1990), which may explain a higher rate of senescence with increasing density. However, there was evidence of density-dependent senescence in males only. Recent experimental evidence does not suggest that density affects the difference in habitat selection between male and female red deer (Conradt *et al.* 1999). This may imply that tooth wear rates alone are not sufficient for explaining the sex-specific, density-dependent senescence pattern, but, possibly, density-dependent food selection may occur despite no density-dependent change in habitat use. Clearly, empirical evidence of a possible difference in density-dependent tooth wear rates for males and females should be looked for.

(b) Density dependence

The debate about the relative role of density dependence versus density independence (e.g. Putman *et al.* 1996; Post & Stenseth 1999) possibly also reflects methodological difficulties in establishing density dependence in a statistically valid way. Our analysis revealed clear evidence of a negative relationship between local density and body weight in Norwegian red deer and this result was also robust when including climate, as measured by the NAOs (see Post *et al.* 1997) in the model. This contrasts with Post *et al.* (1997) who found no evidence of density dependence when using the total harvest in six main regions in Norway as an index of population size on a smaller data set from the same region, but supported the conclusion of Loison *et al.* (1999*b*) for a subpopulation (Snillfjord municipality) in Sør-Trøndelag entering year (as a continuous variable) as an index for density (see §2(c)). Our analysis also showed clear density dependence when using either the total harvest in Norway or year (as a continuous variable) as an index for density. The finer spatial scale used in this study was thus

responsible for our different result. It has been demonstrated earlier that local population density was more important than total population density in influencing calf winter survival on Rum, Scotland (Coulson *et al.* 1997) and scale-dependent population dynamics have also been demonstrated for Soay sheep on Hirta in the St Kilda archipelago (Coulson *et al.* 1999). Similarly, when using the local municipality scale, we found opposite results to Post *et al.* (1999) as to how density affected sex-ratio variation in red deer (Mysterud *et al.* 2000), which supported Kruuk *et al.*'s (1999) conclusion that, with increasing density, male-biased offspring are decreasingly produced. Although the total harvest in Norway has increased, this is a result of both increased density and range expansion (Mysterud *et al.* 2000). The spatio-temporal scale also proved important for the analysis of the data set on Norwegian red deer body weight presented here. This data set sometimes contains data from different municipalities from year to year and the spatial variability in body weight was somewhat stronger than the temporal variability due to density and the NAO (table 1). In addition, there is at present no evidence that density has affected juvenile survival in Norwegian red deer (Loison & Langvatn 1998) and density dependence in fecundity was suggested to be low, although not directly tested for (Langvatn *et al.* 1996). This seems to contrast to the strong density dependence in fecundity (Albon *et al.* 1983; Clutton-Brock *et al.* 1987*a*) and juvenile survival (Clutton-Brock *et al.* 1987*b*; Coulson *et al.* 1997) reported from Rum, Scotland. The Norwegian red deer population is thus probably still at a relatively low density compared to Rum, but continued population growth at the present rate will probably also soon lead to density dependence in these demographic traits.

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