

Relationships in red deer *Cervus elaphus* mandibles

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Growth in mammals often implies differences in body proportions and tissue development more or less characteristic for different age periods and ontogenetic stages. Mouth morphology is an important functional trait in herbivores, as it may determine both maximal intake rate and possibly level of selectivity. An untested hypothesis is that since individual bones within the skeleton are retarded in growth and development in proportion to their growth intensity at each time interval during periods of restricted nutritional supply, this may potentially affect ultimate skeletal proportions. We analysed data on mandible proportions (anterior:total) of 62 fetuses collected at different stages of growth and 16776 red deer *Cervus elaphus* Linnaeus, 1758 hinds from 0 to 26 years of age and 24026 males from 0 to 22 years of age harvested during autumns 1965–2001 along the west coast of Norway. At the fetal stage, the mandible proportion was negatively related to body weight and, therefore, declined with age of the fetus. The anterior part of the mandible was initially longer than the posterior part; the mandible proportion was between 0.75–0.8 at the fetal stage, but declined with increasing age. The relationship between mandible proportion and weight was strong for calves, but decreased with increasing age, and the relationship was almost flat when reaching 5 years of age. From 5 years, the anterior and posterior part of the mandible was approximately equal in length and this mandible proportion (0.50–0.51), which was unrelated to weight, remained stable for the rest of the life in both hinds and stags. After they were fully-grown, early conditions (cohort density and climate as measured by the North Atlantic Oscillation) had no measurable effect on ultimate mandible proportions after the effect of body weight was removed.

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Introduction

Growth in mammals often implies differences in body proportions and tissue development more or less characteristic for different age periods and ontogenetic stages. Classic studies on domestic species have demonstrated that growth follows a centripetal pattern caused by waves of high growth intensity commencing in distal

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parts of body extremities and converging along the back line towards the pelvic region (Hammond 1932, Hammond 1940, McMeekan 1940, Walker 1964). This pattern is described as a change in timing of differentially declining growth rates of specific parts of the body (Wallace 1948), which explain the progress of the proximodistal-distoproximal pattern in the limbs, and craniocaudal-cranionasal pattern in the axial skeleton (Hammond 1940, McMeekan 1940, Davies *et al.* 1984). Differences in timing for maturation and growth intensity in various organs seem to be associated with their functional importance both in pre- and post natal life (Wenham and Pennie 1986). Although species differences occur (Hammond 1940, Davies *et al.* 1984), the general pattern applies to most large mammals and tissues over the entire ontogenetic process (Wallace 1948).

At any given stage, an organ or part of tissue with high growth intensity at the time appears to be more affected by nutritional or energetic restriction than organs or tissues which either have passed or not yet reached the period of high growth priority (Hammond 1940). Consequently, it can be assumed that body size and composition, together with skeletal parts representing both early and late maturing tissues, may reflect environmental conditions and resource access. Early development has been shown to have lasting effects on fitness in birds and mammals (review in Lindström 1999), and evidence of cohort effects in vital rates in cervids are common (review in Gaillard *et al.* 2003). An untested hypothesis is that early conditions (eg, related to cohort differences in nutritional supply) may potentially affect ultimate skeletal proportions (Pálsson and Vérges 1952a, b).

In ungulates, the morphology of the mouth is important in determining maximal intake rates in grazers and possibly selectivity in browsers (Gordon and Illius 1988, Illius and Gordon 1990). Factors determining the morphology of associated structures are, therefore, likely to be functionally important to the herbivore (Illius and Gordon 1990). The relationship between total and mandibular size and age has long been studied in red deer *Cervus elaphus* Linnaeus, 1758 (Mystkowska 1966, Dzieciółowski 1970, Lowe 1972, Azorit *et al.* 2003), and the breadth of the incisor arcade relative to body weight changed during growth (Illius and Gordon 1990). Here, we examine relationships between the anterior (early maturing) and posterior (late maturing) part of the mandible and age and body weight of male and female red deer. This includes data from 62 fetuses collected at different stages of growth and 16776 red deer hinds from 0 to 26 years of age and 24026 males from 0 to 22 years of age harvested during autumns 1965–2001 along the west coast of Norway. We provide a description of the growth pattern of the anterior and posterior part of the mandible, and we test whether early conditions (related to cohort density and climate as measured by the North Atlantic Oscillation; NAO) give rise to differences in ultimate mandibular proportions.

Material and methods

Study area

The study area is the western part of southern Norway, which is the main area for red deer in Norway (Myrsterud *et al.* 2000). Data derive from 108 municipalities (size 48–2702 km²) in the counties Rogaland ($n = 6$) and Hordaland ($n = 23$; referred to as population P1), Sogn og Fjordane ($n = 24$; population P2), Møre og Romsdal ($n = 29$) and Sør-Trøndelag ($n = 19$; population P3) and Nord-Trøndelag ($n = 7$; population P4). The island Hitra is referred to as population P5 (eg, Myrsterud *et al.* 2001a). The habitat (Myrsterud *et al.* 2002) and topography (Myrsterud *et al.* 2001a) is described in detail elsewhere.

Red deer data

Red deer were sampled during the annual autumn harvest 1965–2001 (between 10 September and 15 November) in 108 different municipalities, including 16776 red deer hinds from 0 to 26 years of age and 24026 males from 0 to 22 years of age (Table 1). Hunting is controlled through sex and age-specified licenses issued by local wildlife boards in each municipality. Hunters provided mandibles from all animals shot, together with records of sex, date, locality (municipality) and body weight. The age of calves and yearlings was determined from tooth eruption patterns (Loe *et al.* 2004), whereas older animals were aged on the basis of dental-cementum annuli in the root of the first incisor (Reimers and Nordby 1968, Hamlin *et al.* 2000). Body weight is dressed weight (58% of live weight), ie live weight minus head, skin, viscera, bleedable blood and metapodials (Langvatn 1977). The data on body weight has been used previously (Langvatn and Albon 1986, Langvatn *et al.* 1996, Post *et al.* 1997, 1999, Myrsterud *et al.* 2001a, b, c, 2002, Yoccoz *et al.* 2002, Loe *et al.* 2003).

In addition, data on 62 fetuses collected from October through June were available. These were from hinds that had died in traffic accidents, shot at pests on agricultural land or had been shot for scientific purposes. Data on weight for fetuses are total weight.

Measurement of mandibles

Following Langvatn (1977), we measured, with a vernier-caliper, the (1) anterior part of the mandible [the length of the front part of the mandible measured from the most oral-medial point at the socket of the first incisor, anterior-ventral side (K; Fig. 1), to the most anterior-oral point at the socket of the first molar, buccal side (L; Fig. 1)] and the (2) posterior part (the length from L to the most posterior point at *processus angularis*, M; Fig. 1). The sum of the anterior and posterior comprised the full length of the mandible, and we refer to mandible proportion as length of anterior part to length of total mandible.

Measures of early conditions – cohort density and climate

To obtain a density index that reflect both spatial and temporal components of density, we divided total number of red deer harvested each year by the so-called “qualifying area” in each municipality (used area for 2001 for all years; Statistics Norway 2001; approach as in Myrsterud *et al.* 2001c). 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. Cohort density index was defined as the number of harvested red deer in the year of birth of an individual deer divided by the “qualifying area” (for year 2001) (Myrsterud *et al.* 2002). During the study period, the red deer population has been increasing steadily, and the harvest has increased 10-fold (and the number of deer killed in traffic also; Statistics Norway 2002, even after controlling for increase in traffic; Myrsterud 2004). Body weights are still decreasing (Myrsterud *et al.* 2001c, 2002, R. Langvatn, unpubl.), indicating that the population size is still increasing relative to resource availability, ie, we have not yet reached a situation of overharvesting.

Table 1. Sample sizes (n) of red deer mandibles sampled during autumns 1965-2001 along the west coast of Norway. Average length (\bar{x} mm) of anterior and posterior parts of the mandible and standard error (SE), as well as the proportion (anterior : total) is given for each age class.

		Age																											
		0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	
		Females																											
n		3195	3550	2732	2190	1038	811	666	554	403	329	248	219	177	137	128	101	69	58	45	39	35	17	13	7	11	3	1	
Anterior part		\bar{x}	114	132	135	137	138	138	139	139	139	140	140	139	140	139	140	140	140	140	140	139	140	140	142	141	141	138	143
	SE	0.08	0.07	0.08	0.09	0.13	0.15	0.17	0.19	0.22	0.24	0.27	0.30	0.33	0.36	0.38	0.43	0.50	0.59	0.64	0.68	0.77	1.00	1.18	1.62	1.32	2.64	4.58	
Posterior part		\bar{x}	70.6	105	123	130	133	135	136	136	137	137	137	138	138	138	138	139	139	138	136	139	139	139	137	140	141	142	
	SE	0.09	0.08	0.1	0.11	0.16	0.18	0.20	0.21	0.25	0.28	0.32	0.34	0.38	0.43	0.45	0.50	0.61	0.66	0.75	0.81	0.85	1.23	1.40	1.91	1.52	2.92	5.05	
Proportion		\bar{x}	0.619	0.556	0.525	0.512	0.508	0.505	0.504	0.504	0.504	0.504	0.504	0.502	0.503	0.502	0.502	0.502	0.503	0.502	0.502	0.502	0.502	0.502	0.504	0.507	0.502	0.493	0.502
	SE	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.002	0.002	0.002	0.003	0.004	0.003	0.006	0.010
		Males																											
n		4030	7941	5951	3093	1232	675	422	225	173	109	58	49	26	16	9	8	3	1	3	1							1	
Anterior part		\bar{x}	116	137	142	145	147	148	148	149	149	149	150	150	147	149	150	147	148	139	147	145							155
	SE	0.08	0.05	0.06	0.09	0.14	0.19	0.24	0.32	0.37	0.47	0.64	0.71	0.94	1.21	1.48	1.62	2.96	5.13	2.57	5.13								5.13
Posterior part		\bar{x}	72	110	129	139	143	145	147	147	147	149	148	147	145	146	149	146	148	140	143	142							142
	SE	0.09	0.06	0.07	0.10	0.16	0.22	0.28	0.38	0.43	0.54	0.74	0.81	1.11	1.41	1.88	2.00	3.26	5.65	3.26	5.65								5.65
Proportion		\bar{x}	0.619	0.555	0.523	0.511	0.506	0.504	0.502	0.503	0.500	0.503	0.504	0.503	0.503	0.505	0.502	0.499	0.501	0.498	0.500	0.505							0.522
	SE	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.001	0.001	0.001	0.001	0.002	0.003	0.003	0.004	0.006	0.010	0.006	0.010								0.010

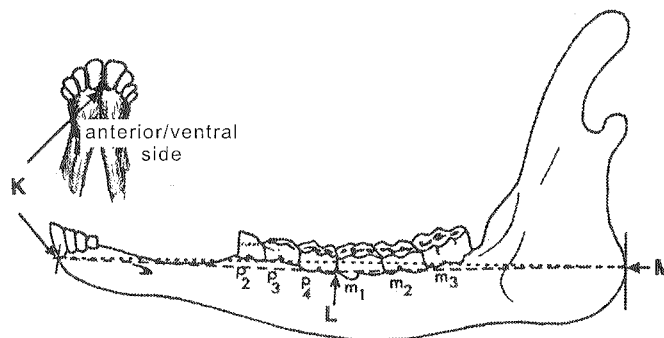


Fig. 1. A red deer mandible with arrows indicating anterior (K–L) and posterior (L–M) parts. The mandible proportion is defined as anterior length to total length.

As a descriptor of the overall climatic environment, we used the station-based winter (Dec–Mar) index of the North Atlantic Oscillation (NAO; Hurrell 1995, Hurrell *et al.* 2002), which is known to influence performance of red deer in Norway (Post *et al.* 1997, 1999, Mysterud *et al.* 2001b; reviews in Stenseth *et al.* 2002, 2003, Mysterud *et al.* 2003). We used the NAO when *in utero* (cohort NAO: Post *et al.* 1997) and for the previous winter (ie, same year as harvested; Mysterud *et al.* 2001b).

Statistical analyses

For fetuses, we used two models (ANCOVA), one analyzing mandible proportion relative to date (ie, age) and the other relative to total body weight, with sex as a factor in both models. Mandible proportions were transformed $\{\arcsin[\sqrt{\text{mandible proportion}}]\}$ before analyses.

For the main data set, we used sex-specific models, and we first prepared descriptive data on length of anterior and posterior parts of the mandibles as well as mandible proportion for each age group using adjusted (least-square) means (Venables and Ripley 1994). In order to correct for possible bias (cfr. Cochran and Rubin 1973) due to imbalance in the study design (not an equal amount of data from each municipality each year), we also included covariates that are known to affect body weight. These were date of culling (Yoccoz *et al.* 2002), distance from the coast, and degree of latitude (Langvatn and Albon 1986, Mysterud *et al.* 2001a), proportion of high altitude habitat, diversity of altitudes and aspects (Mysterud *et al.* 2001a), the density index (Mysterud *et al.* 2001c), the NAO (Mysterud *et al.* 2001b) and “population” (Forchhammer *et al.* 1998). Note that populations 1 to 4 go from south to north and therefore partly account for effects of the degree of latitude.

To accurately determine at what age the growth of the anterior and posterior part of the mandible stopped, and hence the mandible proportion stabilized, for each sex, we entered age as a factor (older animals classified as 10 years) and used the “treatment” contrast within a linear modelling setting that adjusted for multiple comparisons (ie a family-wise comparison with the Tukey method in S-Plus; Venables and Ripley 1994). The same covariates as mentioned above were included also in these models.

Then, for each sex, we separated data into two further analyses; one for the period before stabilization in mandible proportion, and one for the period after. For the first period, we were mainly interested in the relationship between mandible proportion and body weight for each age class. As age classes differ in weight, we standardized (mean = 0, SD = 1) first weight within each age class to make them comparable (this is equivalent to looking at residuals relative to mean weight within each age class). For the second, we were mainly interested in lasting effects related to cohort density and climate (see above). Analyses were done in S-Plus (Venables and Ripley 1994).

Results

Mandible ratios in fetuses declined markedly with date for both sexes (Fig. 2A, $n = 51$, Table 2). This was due to the fact that mandible proportions declined with

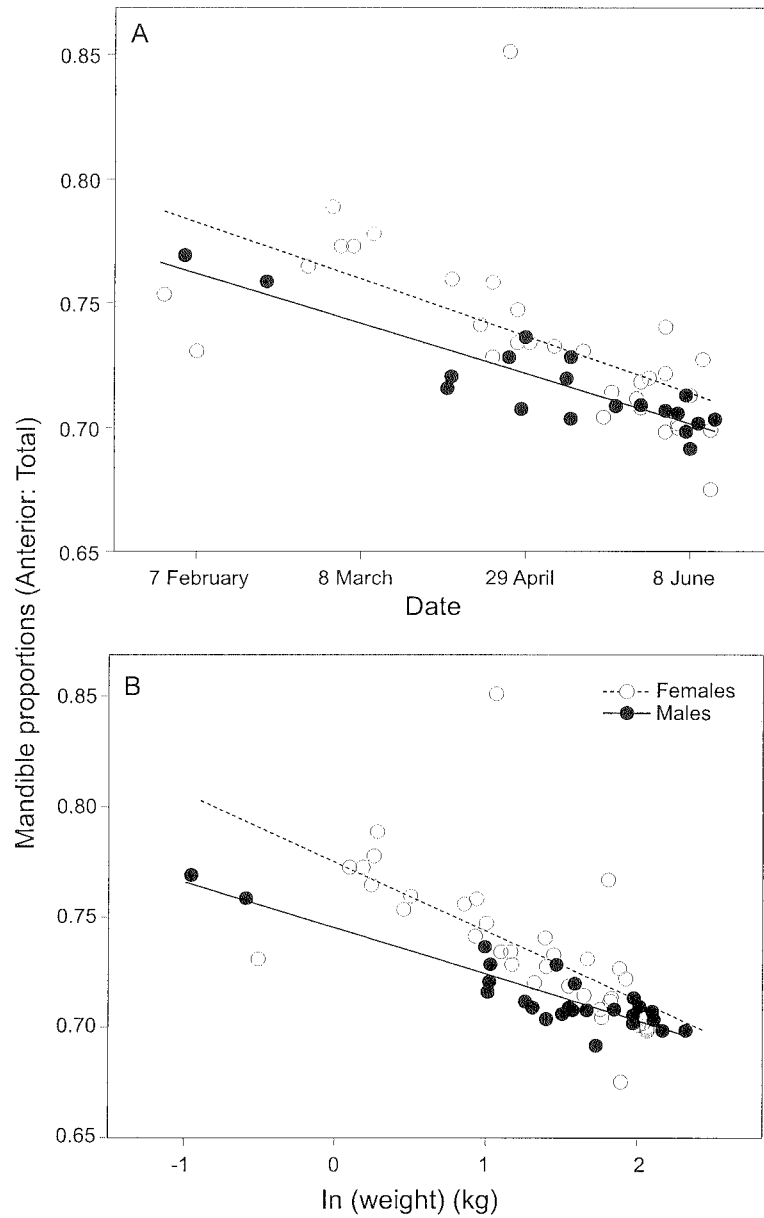


Fig. 2. The relationship between mandible proportion and date (A) and body weight (B) in red deer in prenatal life.

Table 2. Results of analyses (ANCOVA) of mandible proportions in red deer fetuses from the west coast of Norway (A: $n = 51$, B: $n = 62$).

	L.s. estimate	SE	95% C.I.	
			Lower limit	Upper limit
A. Date model				
Intercept	1.1338	0.0209	1.0919	1.1756
Date	-0.0006	0.0001	-0.0008	-0.0004
Sex	-0.0163	0.0209	-0.0581	0.0255
Sex*Date	0.0000	0.0001	-0.0002	0.0003
B. Weigth model				
Intercept	1.0591	0.0067	1.0456	1.0726
ln(Weigth)	-0.0298	0.0044	-0.0386	-0.0210
Sex	-0.0173	0.0067	-0.0307	-0.0038
Sex*ln(Weigth)	0.0060	0.0044	-0.0028	0.0147

increasing body weight (Fig. 2B, $n = 62$, Table 2), and there was no residual effect of date after accounting for body weight (l.s. mean = 0.000047, SE = 0.000073). For a given body weight females had higher mandible proportions than males (Fig. 2; Table 2); at a given date of culling, females only tended to have higher mandible proportions than males (Table 2).

After birth, both portions of the mandible increased non-linearly with age in males and females (Table 1, Fig. 3). In both sexes, rate of growth in the anterior portion of the mandible was slower than that in the posterior portion (Table 1, Fig. 3). Growth in the anterior and posterior part and a change in the mandible proportion could no longer be detected after an age of 5 and 6 years in both sexes (Fig. 4).

The relationship between mandible proportion and weight was strong for calves, but decreased with increasing age (Table 3, Fig. 5). The relationship was almost flat when reaching 4–5 years of age. From 5 years, the anterior and posterior part of the mandible was approximately equal in length and this mandible proportion (0.50–0.51) remained stable for the rest of the life in both hinds and stags. There was no effect of weight on mandible proportion for animals above 6 years of age. Further, after they were fully-grown, early conditions (cohort density and climate as measured by the North Atlantic Oscillation) had no measurable effect on ultimate mandible proportions (Table 4).

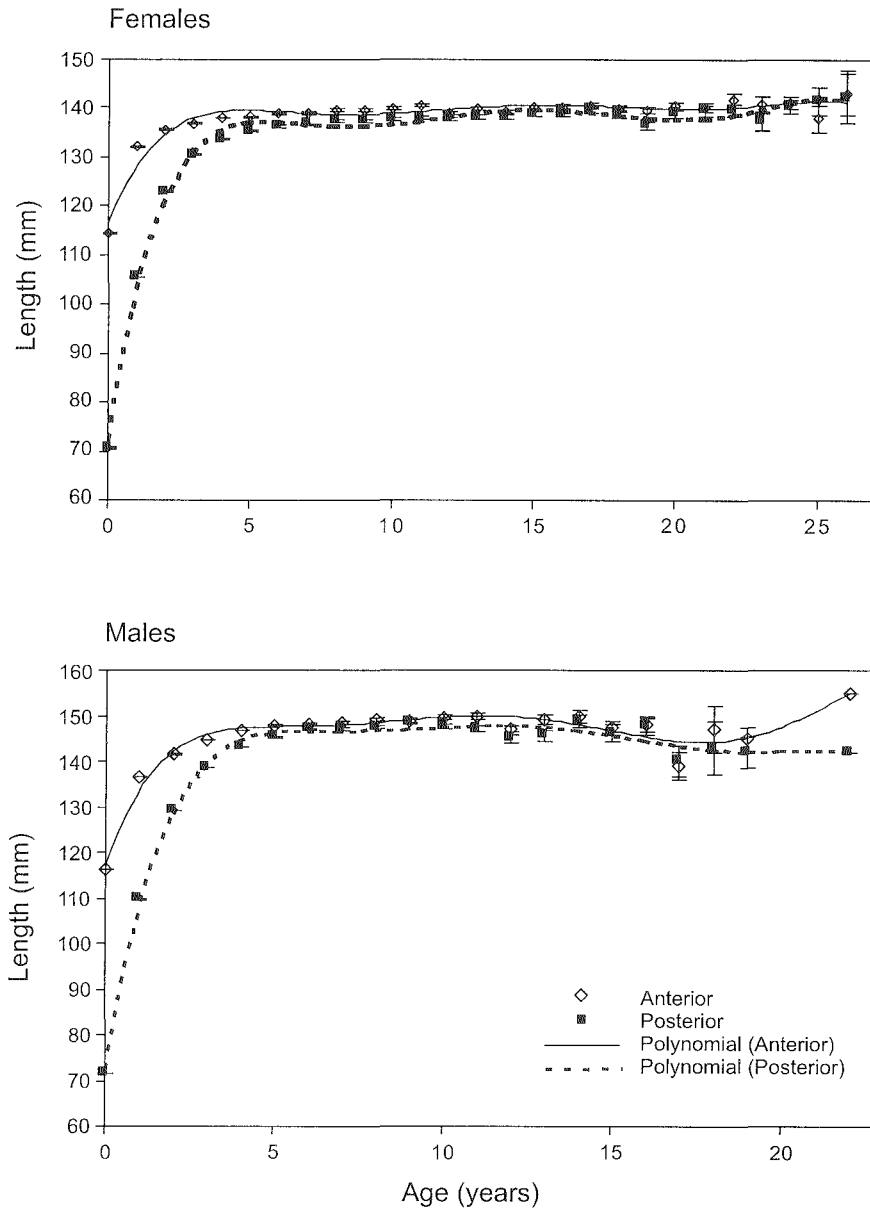


Fig. 3. Growth of the anterior and posterior part of the mandible for female and male red deer harvested during autumns 1965–2001 along the west coast of Norway. Point estimates are age-specific estimates (\pm SE), while the line is a 6th order polynomial for age.

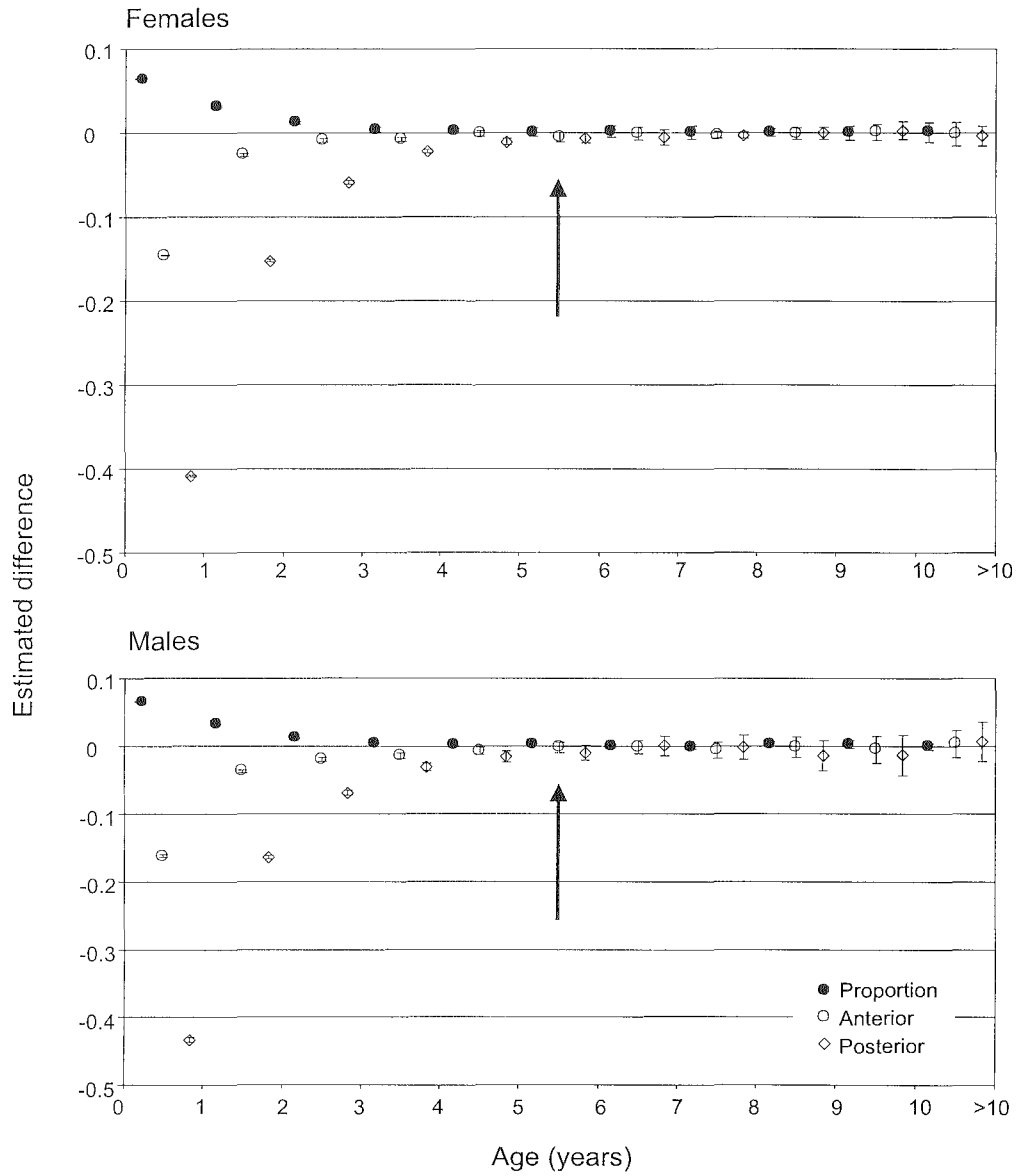


Fig. 4. Test results (multiple comparison; Tukey method) showing estimated differences (and 95% CI) in mandible proportions, anterior and posterior mandible parts from one age class to the next for females and males. Confidence intervals not overlapping zero indicates a significant change between age classes compared. Arrows indicate the transition from a significant change to no change.

Table 3. Correlation between body weight and mandible proportion (transformed) in red deer and its interaction with age in female and male red deer. Results form the basis of figure 5.

	LS. estimate	SE	95% C.I.	
			Lower limit	Upper limit
Females				
Intercept	0.5932	0.0325	0.5281	0.6582
Weight (st. within age groups)	-0.0110	0.0003	-0.0116	-0.0104
Age (1 vs 0)	-0.0228	0.0004	-0.0237	-0.0219
Age (2 vs 0)	-0.0339	0.0005	-0.0349	-0.0329
Age (3 vs 0)	-0.0402	0.0005	-0.0412	-0.0392
Age (4 vs 0)	-0.0440	0.0007	-0.0454	-0.0427
Age (5 vs 0)	-0.0457	0.0007	-0.0472	-0.0443
Age (>5 vs 0)	0.0678	0.0004	0.0669	0.0686
Date of culling	0.0000	0.0000	0.0000	0.0000
Distance from the coast	0.0043	0.0004	0.0035	0.0052
Density	-0.0030	0.0004	-0.0038	-0.0021
NAO	0.0002	0.0001	0.0000	0.0003
Population(P2-P1)	0.0038	0.0004	0.0030	0.0046
Population(P3-P1)	0.0033	0.0004	0.0025	0.0042
Population(P4-P1)	0.0045	0.0019	0.0006	0.0083
Population(P5-P1)	-0.0096	0.0012	-0.0120	-0.0073
Diversity of altitudes	-0.0023	0.0009	-0.0041	-0.0005
Proportion of high altitude habitat	0.0027	0.0011	0.0006	0.0049
Diversity of aspects	0.1162	0.0157	0.0847	0.1476
Weight (st. within age groups)*Age (1 vs 0)	0.0068	0.0005	0.0059	0.0077
Weight (st. within age groups)*Age (2 vs 0)	0.0088	0.0005	0.0079	0.0097
Weight (st. within age groups)*Age (3 vs 0)	0.0099	0.0005	0.0090	0.0109
Weight (st. within age groups)*Age (4 vs 0)	0.0108	0.0006	0.0096	0.0121
Weight (st. within age groups)*Age (5 vs 0)	0.0101	0.0007	0.0087	0.0114
Weight (st. within age groups)*Age (>5 vs 0)	-0.0026	0.0004	-0.0035	-0.0017
Males				
Intercept	0.8942	0.0154	0.8634	0.9250
Weight (st. within age groups)	-0.0077	0.0002	-0.0080	-0.0074
Age (1 vs 0)	-0.0667	0.0002	-0.0671	-0.0663
Age (2 vs 0)	-0.0983	0.0002	-0.0987	-0.0979
Age (3 vs 0)	-0.1103	0.0002	-0.1107	-0.1098
Age (4 vs 0)	-0.1146	0.0003	-0.1152	-0.1139
Age (5 vs 0)	-0.1165	0.0004	-0.1173	-0.1157
Age (> 5 vs 0)	-0.1179	0.0003	-0.1185	-0.1172
Date of culling	-0.0001	0.0000	-0.0001	-0.0001
Distance from the coast	0.0013	0.0002	0.0009	0.0017
Density	0.0006	0.0002	0.0002	0.0010
NAO	0.0000	0.0000	0.0000	0.0001
Population(P2-P1)	0.0008	0.0002	0.0005	0.0012
Population(P3-P1)	-0.0012	0.0002	-0.0016	-0.0008
Population(P4-P1)	-0.0038	0.0008	-0.0053	-0.0023
Population(P5-P1)	-0.0026	0.0005	-0.0035	-0.0016
Diversity of altitudes	-0.0004	0.0004	-0.0011	0.0004
Proportion of high altitude habitat	0.0007	0.0005	-0.0002	0.0016
Diversity of aspects	0.0070	0.0075	-0.0079	0.0219
Weight (st. within age groups)*Age (1 vs 0)	0.0052	0.0002	0.0048	0.0056
Weight (st. within age groups)*Age (2 vs 0)	0.0062	0.0002	0.0058	0.0066
Weight (st. within age groups)*Age (3 vs 0)	0.0071	0.0002	0.0067	0.0076
Weight (st. within age groups)*Age (4 vs 0)	0.0080	0.0003	0.0073	0.0086
Weight (st. within age groups)*Age (5 vs 0)	0.0074	0.0004	0.0066	0.0082
Weight (st. within age groups)*Age (> 5 vs 0)	0.0074	0.0003	0.0068	0.0081

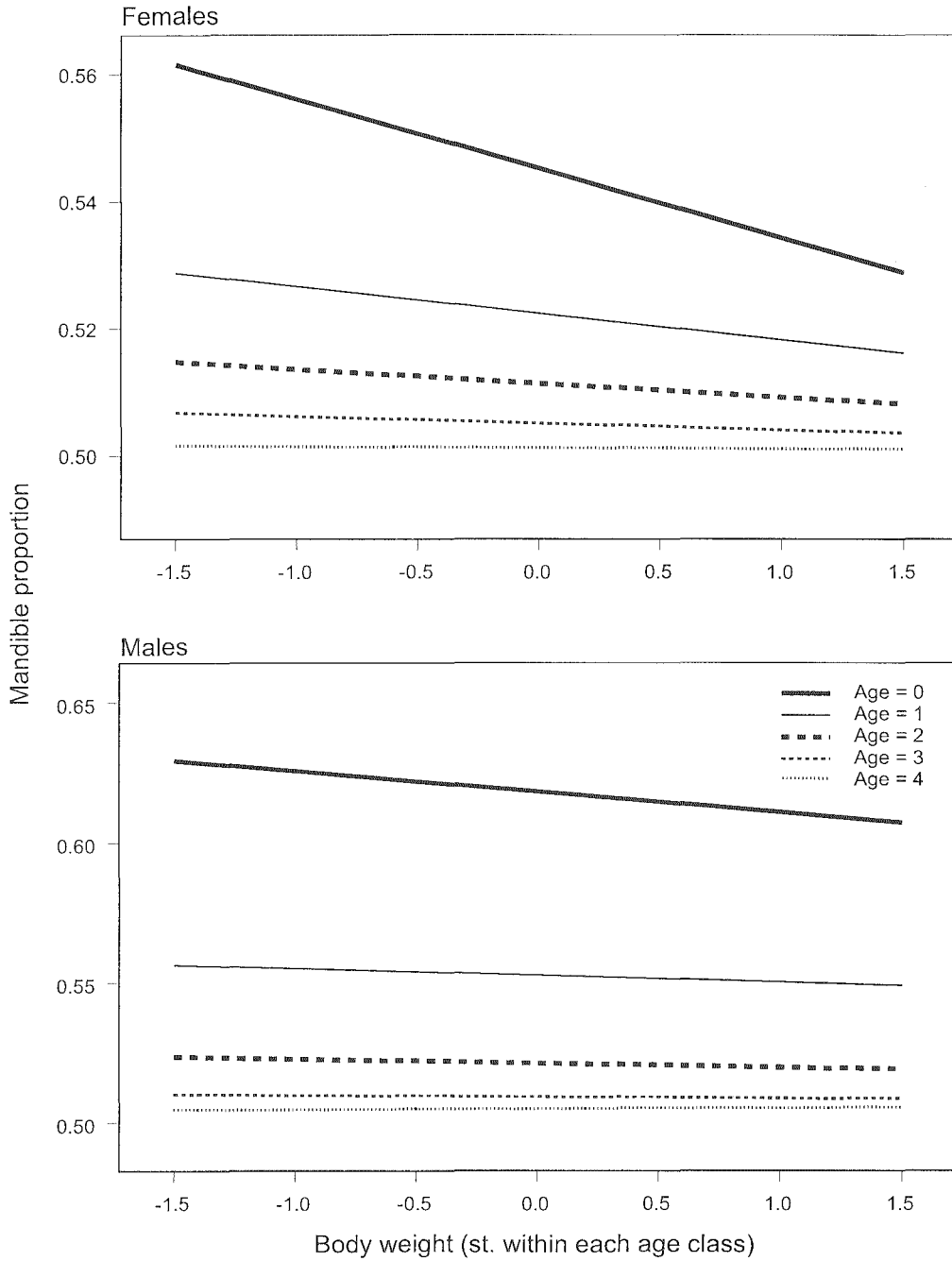


Fig. 5. Declines in the mandible proportion (anterior: total length) with increasing body weight (kg) in females and males.

Table 4. Analysis of mandible ratios in fully grown red deer harvested along the west coast of Norway.

	LS. estimate	SE	95% C.I.	
			Lower limit	Upper limit
Females (> 6 yrs)				
Intercept	0.7651	0.0414	0.6823	0.8479
Age	-0.1027	0.2809	-0.6646	0.4591
(Age) ²	-0.0176	0.1508	-0.3191	0.2840
(Age) ³	0.0279	0.0548	-0.0817	0.1375
Body weight	0.0011	0.0014	-0.0017	0.0040
Date of culling	0.0000	0.0000	0.0000	0.0000
Distance from the coast	0.0006	0.0005	-0.0005	0.0017
Current density	0.0007	0.0008	-0.0008	0.0023
Cohort density	-0.0006	0.0014	-0.0034	0.0021
Previous NAO	0.0002	0.0001	0.0000	0.0003
Cohort NAO	-0.0001	0.0001	-0.0003	0.0001
Population(P2-P1)	0.0036	0.0005	0.0026	0.0046
Population(P3-P1)	-0.0014	0.0006	-0.0025	-0.0003
Population(P4-P1)	-0.0013	0.0023	-0.0059	0.0034
Population(P5-P1)	-0.0010	0.0016	-0.0042	0.0022
Diversity of altitudes	0.0017	0.0012	-0.0007	0.0041
Proportion of high altitude habitat	-0.0019	0.0013	-0.0045	0.0008
Diversity of aspects	0.0081	0.0200	-0.0319	0.0481
Males (> 6 yrs)				
Intercept	0.8121	0.0985	0.6151	1.0091
Age	-0.7868	1.4302	-3.6472	2.0736
(Age) ²	0.4648	0.7459	-1.0270	1.9565
(Age) ³	-0.4689	0.4621	-1.3931	0.4553
Body weight	0.0008	0.0020	-0.0033	0.0048
Date of culling	0.0000	0.0000	0.0000	0.0001
Distance from the coast	0.0019	0.0012	-0.0006	0.0044
Current density	0.0015	0.0015	-0.0015	0.0046
Cohort density	0.0002	0.0029	-0.0055	0.0060
Previous NAO	0.0000	0.0002	-0.0004	0.0004
Cohort NAO	0.0002	0.0002	-0.0002	0.0006
Population(P2-P1)	0.0011	0.0011	-0.0011	0.0033
Population(P3-P1)	-0.0011	0.0012	-0.0036	0.0014
Population(P4-P1)	0.0019	0.0042	-0.0064	0.0103
Population(P5-P1)	-0.0043	0.0030	-0.0104	0.0017
Diversity of altitudes	-0.0016	0.0024	-0.0065	0.0032
Proportion of high altitude habitat	0.0035	0.0033	-0.0030	0.0100
Diversity of aspects	-0.0113	0.0478	-0.1070	0.0844

Discussion

Evidence for strong effects of early conditions on future fitness is pervasive (Lindström 1999). We tested the idea that ultimate mandible proportions (anterior part:total length) may be affected by nutritional supply in early life, since individual bones within the skeleton are retarded in growth and development in proportion to their growth intensity at each time interval (Pálsson and Vérges 1952a, b). Although the mandible proportion changed from around 0.8 at the fetal stage to around 0.5 at 5 years of age, we found no evidence that ultimate mandible proportions were affected by early (cohort) conditions. As our data are transversal, we cannot fully exclude the possibility that our result is due to stabilizing selection on this trait, if individuals with disproportionate mandible ratios are more prone to die in early stages of life. However, we regard this as less likely, since changes in mandible ratios are seen up to 5–6 years of age, and survival is high from 2 to 5 years of age (Langvatn and Loison 1999, review in Gaillard *et al.* 1998).

Within the axial skeleton, the cranium surrounding the brain is the earliest part to develop, showing high growth intensity already in fetal life (Pálsson and Vérges 1952a, b). From the cranium, waves of temporally high growth intensity pass backwards to the lumbar region and forward to the nose and lower jaw. At birth, *in utero* low-plane lambs showed that early-maturing metapodials, with a high growth priority in fetal life, are relatively less developed than other bones, whereas in post-natal life, late-maturing bones like femur are proportionately more affected in lambs on adequate nutritional supply during pregnancy, but on a subsequent low-plane diet (Pálsson and Vérges 1952a, b). Mandible proportion correlated significantly with body weight up to 2 years of age in red deer, and mandible proportion, therefore, probably differed between cohorts. However, there was no residual effect of adverse conditions, measured as cohort density and cohort NAO, related to their first year of life after the effect of body weight was controlled for.

The very strong ontogenetic changes in relationship in red deer mandibles is interesting since it has been claimed that such pattern reflect functional importance both in pre- and post-natal life (Wenham and Pennie 1986). Does different proportions in red deer mandibles have functional implications for ungulate foraging ecology? It is well known that body size is very important for foraging ecology. Large herbivores can survive on a lower quality diet than smaller ones; since the relative energy requirements decrease with increasing body-size ($\text{Weight}^{0.75}$) and rumen volume is isometric with size (Jarman-Bell principle; Bell 1971, Jarman 1974, Geist 1974). Smaller ruminants should, therefore, be more selective than larger ones (Demment and Van Soest 1985). Red deer is a mixed feeder (Hofmann 1989); eating mainly grasses and some herbs during summer (Albon and Langvatn 1992), while eating more browse during winter in Norway (Ahlén 1965). There is some evidence that the width of the arcade incisor affect maximal intake rate in grazers (eg, Illius and Gordon 1987, Gordon and Illius 1988), and the relationship between the breadth of the arcade incisor and body weight changed during

ontogeny (Illius and Gordon 1990). It has been suggested that the longer "noses", and subsequently the longer mandibles, in browsers compared to grazers may allow browsers to be more selective when foraging on browse (Gordon and Illius 1988). At present, we can only speculate regarding the possible functional role of mandible proportions in affecting herbivore selectivity at different growth stages, but this should be addressed in future studies.

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