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Early developed section of the jaw as an index of prenatal growth conditions in adult roe deer *Capreolus capreolus*

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Increasing evidence suggests that conditions in early life have important consequences for ultimate body size and fitness. Skeletal parts are often used as retrospective indices of body size and growth constraints because of their resistance to seasonal variation in resource availability. Yet, slow-maturing bones are poor predictors of resource limitations during early development, as later benign conditions may lead to compensatory growth. We analysed the temporal growth dynamics of different sections of the lower jaw of roe deer *Capreolus capreolus* and found that the medioanterior section of the lower jaw reaches 95% of asymptotic size already at 2-4 months *post partum*, whereas the posterior section reaches 95% of asymptotic size at 14-16 months *post partum*. Hence, the size of the medioanterior section of the lower jaw is only dependent on resource availability *in utero* and the first few months *post partum* and, as such, potentially leaves a fingerprint of prenatal growth conditions that is evident even in adult individuals. This supports earlier findings in ungulates of a shift in skeletal growth spurts after weaning, and suggests that the choice of skeletal index for population and cohort studies is not trivial.

Key words: *Capreolus capreolus*, cohort effects, development, environmental constraints, growth, jaw

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Body size is an ecological correlate of most life history traits (Calder 1984, Roff 2002), and in game species it is of great economic importance for wildlife managers

(Bolen & Robinson 1995). Hence, much work has been devoted to disentangle the factors governing growth and size differences among individuals and populations.

Factors such as population density (Pettorelli et al. 2002), habitat quality (Bertouille & de Crombrughe 1995), genetic structure (Coltman et al. 2001) and climate (Post & Stenseth 1999) are considered relevant predictors of body size in ungulates. In particular, cohort-specific differences arising through direct abiotic stress and density-dependent resource limitations on mothers during early growth may contribute significantly to adult body size and fitness (Lindström 1999, Forchhammer et al. 2001). However, the consequences of these cohort-specific conditions may not be easily separated from later resource constraints experienced at an individual level. A reliable index of early growth constraints obtainable from cross-sectional population data is therefore needed.

Skeletal parts are widely used indices of body size as size and shape of bones are resistant to seasonal resource variation (Huot 1988). In particular, the lower jaw has been suggested as an index of habitat quality in many deer species, e.g. caribou *Rangifer tarandus* (Ver Hoef et al. 2001), fallow deer *Dama dama* (Nugent & Frampton 1994), red deer *Cervus elaphus* (Bertouille & de Crombrughe 1995) and roe deer *Capreolus capreolus* (Hewison et al. 1996). Also, selection on foraging efficiency has been documented in a wild ungulate as indexed by incisor arcade width (Illius et al. 1995). Thus, in terms of oral capacity larger jaws can be expected to represent better conditions.

The development time of bones used to index growth conditions is of less importance in stable environments, but with varying levels of competition, under changing management practices or climatic changes a fast maturing bone is pertinent as an index, because it restricts the variability in growth conditions responsible for the asymptotic size of the individual skeletal part. For instance, adverse winter conditions while cohorts are *in utero* may precede milder and more favourable conditions in the following winter. This should result in a medium-sized bone if it matures after the second winter and a short bone if it matures before the second winter.

We analysed and contrasted the growth dynamics of different sections of the lower jaw in roe deer to identify a potential index of early growth conditions. We fitted general growth models to size measurements of large samples of aged individuals. In roe deer fawns, the second, third and fourth deciduous premolars are fully developed at birth and are replaced by three permanent premolars and three molars within the first year of life (Strandgaard 1972b). Hence, we hypothesise that the diastema and the anterior section of the post canine tooth row is the first part of the lower jaw to become fully developed and that the size of this index would potentially reflect growth conditions experienced in early life.

Material and methods

Data and measurements

Our data material originates from a long-term study of two populations of roe deer in Denmark at Borris (55°55'N, 08°40'E) and Kalø (56°7'N, 10°30'E; Strandgaard 1972b, Strandgaard 1999) and includes data on 2,386 individuals. A subset of 493 individuals were ear tagged as fawns and hence effectively of known age. The remaining individuals were aged according to a refined method of tooth replacement and wear that provides the correct age of 88% of all individuals 0-4 years old (Høye 2001). Older individuals were not included in the analyses, thus, ensuring high accuracy in age estimates. Staff from the National Environmental Research Institute, Denmark, collected data during 1956-1999 for the Kalø population and during 1963-1992 for the Borris population. The date, year of death and sex were recorded for all individuals and cleaned lower jaws were measured. In the two populations, 80% of births occur between 22 May and 24 June (Strandgaard 1972a). Hence, 1 June was used to determine age in months. Five sections of the lower jaw, i.e. AB, BC, CD, EF and GH (Fig. 1), were measured to the nearest 0.01 mm using a digital slide gauge. Jaw measurements were taken according to Langvatn (1977) and Nugent & Frampton (1994). The right half of the jaw was consistently chosen for measurements; only if this had suffered damage was the left half used (21% of the sample). As a number of jaws had suffered damage during storage, not all sections could be measured on all individuals.

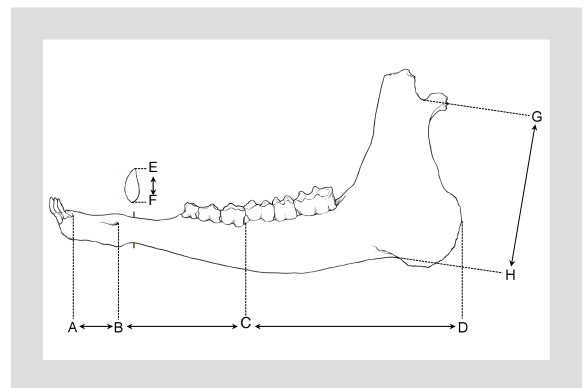


Figure 1. Lower jaw of roe deer with the five sections indicated. AB is the most anterior section of the jaw measured from the posterior margin of the socket of the corner incisor to the posterior margin of the *mental foramen*. BC is the medioanterior section of the jaw measured from the posterior margin of the *mental foramen* to the posterior margin of the posterior-most premolar (PM4). CD is the posterior section of the jaw measured from the posterior margin of the posterior-most premolar (PM4) to the posterior margin of the *processus angularis*. EF is the minimum height of the diastema, and GH is the notch height.

Statistical analysis

We performed 10 repetitions of measurements on six jaws of different size and age measured in random order, and the coefficient of variation was calculated from these repetitions to quantify measurement error. Also, differences between individuals measured on the left and right halves of the jaw were tested in MANOVA with measurements on AB, BC, CD, EF and GH as response variables and jaw side, population and sex as factors for adults (> 36 months old). Mammalian growth has traditionally been described by sigmoid curves (Zullinger et al. 1984, Leberg et al. 1989), but recent comparative work suggests that precocial species may exhibit monomolecular growth after birth as they have their peak growth rate *in utero* (Gaillard et al. 1997); something that is true for post-natal body size development in roe deer (Portier et al. 2000). As developmental rates may vary considerably among skeletal sections, we fitted a flexible Chapman-Richard model (e.g. Gaillard et al. 1997) according to the following equation:

$$W_t = K / \{1 + (m - 1) \exp(a(t_0 - t))\}^{1/(m - 1)}$$

where W_t is the length of the skeletal section at age t , K is the asymptotic size of the skeletal section, m is a shape parameter that locates the inflexion point (on the size axis), a is the relative growth rate, and t_0 is the age at which the inflexion point occurs. This model allows the flexibility of fitting very different growth models using the same equation. By changing the shape parameter m the Chapman-Richard model can be fitted to monomolecular ($m = 0$), Gompertz (m approaches 1) and logistic growth data ($m = 2$). Cross-sectional data, where size is only measured once in each individual, usually exhibit larger variability compared to repeated measurements on the same individuals. Hence, to facilitate convergence of non-linear models we fixed the shape parameter m to 0, 0.99 and 2 and fitted separate models for the three values of m thereby reducing the number of parameters to three. Model fit was compared using Bayesian information criterion (BIC) as recommended to identify the most parsimonious model (Quinn & Keough 2002). We fitted growth models to all data from both populations and sexes together and tested for cohort, population and sex effects in the residuals in a three-way ANOVA. In case of significant population differences we repeated the non-linear regression model fitting and the test of cohort and sex effects for each population separately. To demonstrate whether different sections provide information about different conditions endured during fawn growth we calculated Pearson correlation coefficients for all pair-wise correlations among the five sections of the jaw.

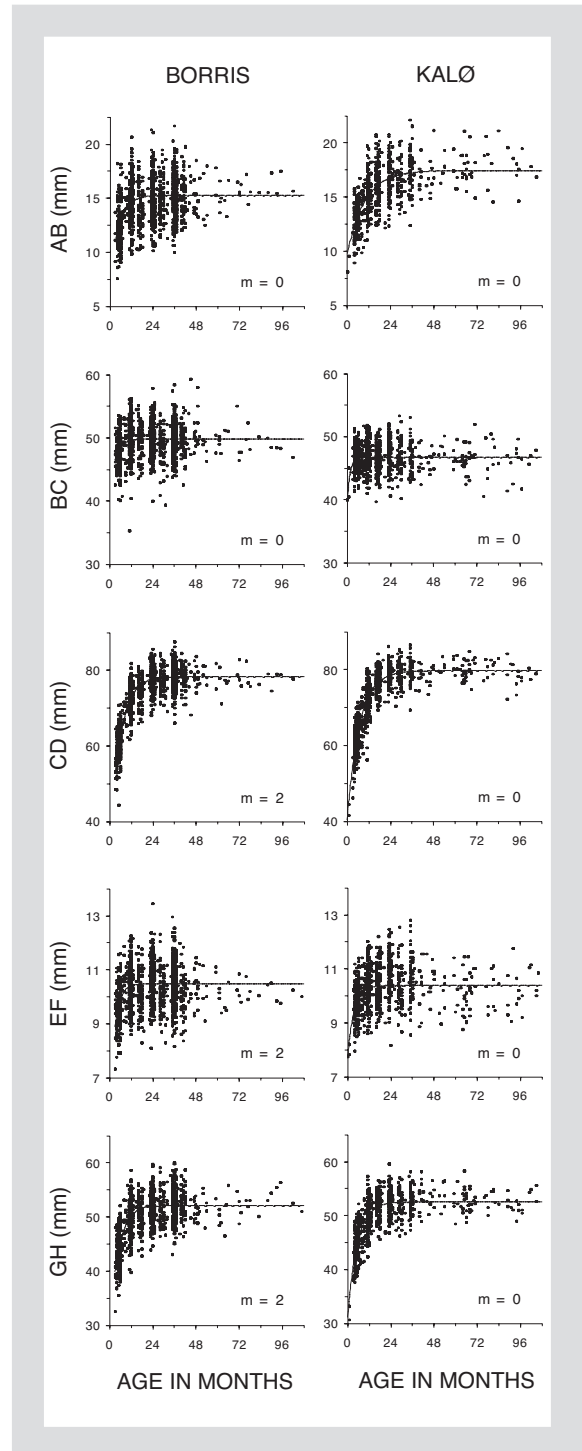


Figure 2. Growth pattern of the five sections (AB, BC, CD, EF and GH) of the lower jaw described in Figure 1 for individuals from the Borris (left subfigures) and Kalø (right subfigures) populations. Black dots are individual observations and full lines are the most parsimonious general Richard-Chapman growth models. Sections where the best fit was obtained by a monomolecular growth form are indicated by $m = 0$ and sections where a logistic growth form gave the best fit are indicated by $m = 2$.

Table 1. Model summary of general Richard-Chapman regression models of the form: $W_t = K / \{1 + (m - 1) \exp(a(t_0 - t))\}^{1/(m-1)}$. Sections refer to skeletal measures illustrated in Figure 1, N is sample size, K is the asymptotic size of the skeletal section, m is a shape parameter that locates the inflexion point (on the size axis), a is the relative growth rate and t_0 is the age at which the inflexion point occurs. Standard errors of model parameters estimated by non-linear regression are given in brackets. The most parsimonious models based on Bayesian information criterion (BIC) was obtained by a monomolecular growth form ($m = 0$ in the General Richard-Chapman model) except for CD, EF and GH from the population at Borris, where a logistic model ($m = 2$) fitted the data significantly better. The age at 95% of asymptotic size is given in months with 95% confidence limits. The significant factors are tested on residuals in two-way ANOVA models with cohort (year of birth) and sex as factors (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$). In case of significant interaction the main effects were not tested.

| Population | Section | N | K | m | a | t_0 | BIC | Residual MS | R-square | Age at 95% of asymptotic size | Significant factors |
|------------|---------|------|-------------------|---|--------------------|-------------------|--------|-------------|----------|-------------------------------|---------------------|
| Borris | AB | 1346 | 15.23 (0.0733) | 0 | 0.217 (0.0259) | -2.829 (0.953) | 5548.2 | 1.882 | 0.20 | 11 (9-13) | Cohort***, Sex** |
| | BC | 1430 | 49.78 (0.0857) | 0 | 0.308 (0.0692) | -5.798 (2.325) | 6700.0 | 2.496 | 0.07 | 4 (3-5) | Cohort:Sex* |
| | CD | 1435 | 78.18 (0.132) | 2 | 0.196 (0.00588) | -1.315 (0.215) | 7489.5 | 3.259 | 0.78 | 14 (13-15) | Cohort*** |
| | EF | 1490 | 10.47 (0.0244) | 2 | 0.360 (0.0519) | -1.831 (0.937) | 3357.2 | 0.740 | 0.14 | 7 (6-8) | Cohort:Sex* |
| | GH | 1358 | 51.99 (0.110) | 2 | 0.238 (0.0136) | -2.000 (0.417) | 6694.7 | 2.819 | 0.52 | 11 (10-12) | Cohort***, Sex*** |
| Kalø | AB | 528 | 17.41 (0.169) | 0 | 0.102 (0.0109) | -8.099 (1.375) | 2076.4 | 1.693 | 0.49 | 23 (20-26) | - |
| | BC | 612 | 46.63 (0.100) | 0 | 0.666 (0.161) | -2.858 (0.974) | 2714.8 | 2.183 | 0.03 | 2 (1-3) | Cohort*, Sex*** |
| | CD | 617 | 79.62 (0.255) | 0 | 0.148 (0.00623) | -4.788 (0.389) | 3309.4 | 3.471 | 0.83 | 16 (15-17) | Cohort*** |
| | EF | 640 | 10.37 (0.0392) | 0 | 0.274 (0.0425) | -5.097 (1.374) | 1416.9 | 0.719 | 0.16 | 6 (5-7) | Cohort***, Sex*** |
| | GH | 595 | 52.48 (0.176) | 0 | 0.191 (0.0126) | -4.720 (0.595) | 2902.9 | 2.722 | 0.63 | 11 (10-12) | Cohort*** |

All statistical analyses were performed using S-Plus 6.1 for Windows (Insightful, Seattle, WA, USA).

Results

The 10 repetitions of measurements on each section of the jaw showed that coefficients of variation did not exceed 0.25% (AB = 0.087%, BC = 0.096%, CD = 0.14%, EF = 0.24% and GH = 0.094%). The measurements of the jaws did not differ in size between the left and right side ($F_{5,217} = 1.65$, $P = 0.148$), but there were significant main effects of sex ($F_{5,217} = 14.94$, $P < 0.001$) and population ($F_{5,217} = 32.78$, $P < 0.001$) among adult individuals. Hence, the measurements are repeatable and do not differ between the left and right side of the jaw.

The five sections (AB, BC, CD, EF and GH) of the lower jaw (see Fig. 1) varied greatly in their dependency on age in both the Kalø and Borris populations. The measurements differed significantly between populations, therefore all measurements and the general Richard-Chapman growth models were plotted against age in months for the two populations separately (Fig. 2). The monomolecular form of the Richard-Chapman model ($m = 0$) fitted data equally well or better than a Gompertz-like ($m = 0.99$) or a logistic model ($m = 2$) in

all sections except CD, EF and GH from the Borris population for which a logistic model gave a better fit based on BIC (Quinn & Keough 2002). In both populations the section BC, hereafter termed the 'medioanterior' section of the jaw, was least dependable on age at Borris ($R^2 = 0.03$; range of R^2 for other sections: 0.14-0.78) and Kalø ($R^2 = 0.07$; range of R^2 for other sections: 0.16-0.83). In fact, the medioanterior section reached 95% of asymptotic size before four months *post partum* in Borris (95% C.I.: 3-5) and before two months *post partum* at Kalø (95% C.I.: 1-3), whereas CD reached 95% of asymptotic size one year later at 14 months *post partum* at Borris (95% C.I.: 13-15) and 16 months *post partum* at Kalø (95% C.I.: 15-17; Table 1). In both populations a significant part of the residual variation could be explained by cohort (year of birth) for all sections except AB from Borris (see Table 1). The effect of cohort was in some cases interacting with the effect of sex, but because of the cross-sectional nature of the data and hence large residual error we did not model sexes separately (see Table 1). Although not independent, all correlations in the correlation matrix of residual variation were significant (Table 2). The later maturing sections CD, EF and GH showed higher correlations coefficients than the early maturing sections, with no section explaining more than 14% of the variation in residuals of BC.

Table 2. Pearson correlation coefficients of residuals from the non-linear regression models pooled for the two populations. All correlation coefficients were significantly different from zero at the 0.001 level. Sample sizes are given in brackets.

| Section | BC | CD | EF | GH |
|---------|--------------|-------------|-------------|-------------|
| AB | -0.23 (1854) | 0.30 (1854) | 0.25 (1867) | 0.30 (1743) |
| BC | - | 0.33 (2042) | 0.26 (2032) | 0.37 (1895) |
| CD | - | - | 0.45 (2038) | 0.61 (1905) |
| EF | - | - | - | 0.51 (1938) |

Discussion

Early developed phenotypic traits may serve as fingerprints of resource limitations during the developmental stage in adult individuals. Previous work has shown that early adverse conditions retard growth of the lower jaw in ungulates, and that this is not fully compensated for later in life (Bertouille & de Crombrughe 1995, Hewison et al. 1996, Metcalfe & Monaghan 2001). Also, cohort variation in jaw indices has been specifically related to global climate change with predictions on life history consequences under future climatic regimes (Post et al. 1997). Clearly, there is great potential in the use of skeletal measures as indices of growth and condition as large samples are readily available, but the use of indices has not been founded in studies of the growth dynamics of different sections of the jaw. Our study demonstrates considerable differences in timing of growth among sections of the lower jaw. Specifically, the medioanterior section (BC in Fig. 1) reaches 95% of asymptotic size before 2-4 months *post partum*, i.e. growth is mainly prenatal, whereas the posterior section (CD in Fig. 1) reaches 95% of asymptotic size about one year later (14-16 months *post partum*). We found strong evidence of cohort variation in all five sections measured. However, the early maturation of the medioanterior section is particularly interesting as it minimises the time window where growth constraints can influence asymptotic size. Thus, it is probably the index least sensitive to changes later in life, and the strongest indicator of resource constraints on foetal development through adverse conditions posed on mothers, as it reaches asymptotic size shortly after parturition. Indeed, after accounting for age dependency we found that only 14% of the variation in BC could be accounted for by any of the other sections. This leads us to believe that the section BC reflects mainly prenatal conditions, whereas CD and the other late-maturing sections reflect post-natal conditions. The lack of short-term fluctuations in growth conditions or the inability of individuals to compensate for adverse early conditions may explain why we did observe cohort effects in all five sections of the jaw.

The functional significance of adult ungulate jaw morphology has been explained mainly as a trade-off between attaining large bite force and the metabolic cost of bone production (Greaves 1988, 1998). However, the diastema is also believed to function as an extension of the oral capacity for food processing which is important in all life stages (Herring 1985, Greaves 1991). Therefore, the medioanterior region can be expected to reach asymptotic size early in life corroborating our analyses. The posterior section of the jaw develops in parallel with the transition in main food source from milk to herbal forage, and this diet shift is likely to have influenced the growth dynamics of the jaw (Herring 1985). Thus, we suggest that the temporal shift in growth spurts between sections of the lower jaw can be explained by the transition in functional demands on the jaw as part of the masticatory apparatus. Indeed, similar growth dynamics have been found in sheep (Todd & Wharton 1934).

Several important implications emerge from our findings. First, to disentangle cohort effects in population dynamics from effects of density dependence and climatic change on adult individuals, we suggest the medioanterior section of the lower jaw as an index of cohort-specific growth constraints. Second, the size of the medioanterior section of the jaw serves as a measurable index of prenatal conditions and hence, it has important applications in population studies and management schemes. Indeed, if a cohort effect in skeletal size can be documented and if it correlates with body condition or reproductive success in adults, it suggests that the population is under physiological stress as individuals are unable to compensate adverse early conditions (Gaillard et al. 2003). Third, we found pervasive cohort variation even in slow maturing skeletal sections indicating that individuals in the populations studied may not be able to recover from adverse early conditions. Fourth, the similar temporal shift in growth spurt in two different populations suggests that it is a general feature of the growth dynamics of the roe deer jaw. Finally, our results also support the idea that the ontogeny of the masticatory apparatus govern the temporal growth development in sections of the jaw (Pond 1977). Hence the use of the medioanterior jaw section as an index of early growth constraints may indeed be applicable for other ungulate species as well. This, however, remains to be investigated.

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