# Modeling growth of mandibles in the Western Arctic caribou herd

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*Abstract:* We compared growth curves for ramus length and diastema length from two autumn collections of mandibles of male Western Arctic Herd caribou in Alaska. We were primarily interested in determining if growth curves of caribou mandibles differed between caribou born during 1959-1967, after the herd had been high for several years and was probably declining in size, and those born during 1976-1988, when the herd was increasing in size. To compare these growth curves, we used a nonlinear model and used maximum likelihood estimates and likelihood ratio tests. We found that growth rates were similar between periods, but intercepts and variances of growth curves differed. From this we infer that calves were smaller in autumn during the 1960s and that significant compensatory growth did not occur later in life.

## Introduction

Mandibles from many species of herbivores have been collected to assess population age structure, recruitment, mortality, and nutritional condition, especially where direct measures of these parameters have been lacking (Banfield, 1955; Alexander, 1958; Klein & Strandgaard, 1972; Lowe, 1972; Miller, 1972, 1974; Reimers, 1972; Doerr, 1979; Beninde, 1988). Mandible length, diastema length, and other skeletal measurements have also been used to determine if body size has changed in populations over time. In most analyses biologists have restricted comparisons to simple statistical tests (e.g., *t*-tests) of mean jaw size of older animals that have finished growing or compared size only within age classes (Skoog, 1968; Doerr, 1979; Valkenburg *et al.*,

1991; Eberhardt & Pitcher, 1992). The primary objective of this study was to determine if nutrition was constraining the Western Arctic Herd during the 1960s when the herd was high and probably declining compared to the late 1970s and 1980s when it was increasing. The only available data from the earlier period were measurements of mandible length and diastema length. Although skeletal measurements are not the most sensitive measures of nutritional constraint in *Rangifer,* severely reduced summer nutrition could be expected to reduce mean growth rates of skeletal measurements (c.f. Skogland, 1990). To compare growth rates of mandibles between periods, we used a nonlinear growth model that included all age classes to determine where the initial restriction in growth

occurred, and whether there was compensatory growth. Because nonlinear statistical methods have not been routinely used in analyses of this kind, we have included a detailed description of the statistical methodology.

## Study area

The Western Arctic caribou herd is presently the largest caribou herd in Alaska (463 000 in 1996), and ranges over 380 000 km2 of roadless tundra and northern boreal forest in the northwestern part of the state (Valkenburg, 1994). Herd size has fluctuated over time with a population low of unknown size in the late 1800s, a population high of 200 000-300 000 (about 0.6-0.8/km²) in the 1960s, and a crash to 75 000 by 1976 from largely unknown causes (Glenn, 1967; Hemming & Glenn, 1968; Skoog, 1968; Davis *et al.*, 1980; Doerr, 1980). From 1976 to about 1990 the herd grew steadily at about 13% per year and then stabilized (Valkenburg *et al.*, 1996; Dau, 1997). In 1990, population size was approximately 416 000 (1.2/km2) (Dau, 1997).

## Methods

### Mandible collections

Mandible collections were available from two periods. The collection of mandibles came primarily from hunter-killed caribou from Anaktuvuk Pass and five other Inupiat villages (primarily on the Kobuk River) in northwestern Alaska. These were taken primarily from autumn-killed males between 1965 and 1968. The 1960s was a period of relatively high (and possibly declining) caribou numbers (Davis *et al.*, 1980). In 1970 the herd was estimated at 242 000 (about 0.7/km²) but may have already been declining. The second collection was from 1977 to 1989 when caribou mandibles came from wolf-killed and hunter-killed caribou during mortality studies (Davis & Valkenburg, 1985), and from animals taken in the annual autumn hunt at the Kobuk River crossing. Because skeletal growth of extremities, including mandibles, continues over winter (Valkenburg *et al.*, 1996), and because few females were represented in the earlier collection, we restricted our comparison to autumn collections of mandibles from males only. There were $n_1=438$ mandibles for the 1960s collection and $n_2=598$ for the 1980s collection. Mandibles

were assigned to an age-class based on the eruption/wear method using known-aged jaws for comparison (Miller, 1972; 1974). Ramus and diastema length were measured to the nearest millimeter (Langvatn, 1977).

### Statistical model

The class of statistical models we assumed for the data is given by

$$Y_{ij} = f_i(x_{ij}) + \varepsilon_{ij},$$

where $Y_{ij}$ is the response (ramus length or diastema length) for the $j$th animal in the ith period, $x_{ij}$ is the age of the $j$th animal in the ith period, $f_i(x_{ij})$ is a function of age for the $i$th period, and $\varepsilon_{ij}$ independently distributed from a normal distribution for the $i$th period; $\varepsilon_{ij} \sim N(0, \sigma^2_i)$. Here, period is $i=1$ if year of birth (YOB) is between 1959 and 1967, and $i=2$ if YOB is between 1976 and 1988.

Because the responses (ramus length and diastema length) are growth variables, we expect them to initially increase rapidly with smaller increases in later years, so we used nonlinear methods. Such a curve is given by

$$f_i(x_{ij}) \equiv \beta_{0i} + \beta_{1i} (1 - \exp(-\beta_{2i}x_{ij})),$$

which has several names including the monomolecular growth model. It is a commonly used model for exponential-type of growth (e.g., Seber & Wild, 1989: 328, and references therein). The intercept for this curve is $\beta_{0i}$. The speed by which the curve reaches the asymptote is governed by $\beta_{2i}$; the larger $\beta_{2i}$, the faster the curve reaches the asymptote, and we will call this the growth rate parameter. The amount of growth (beyond that given by the intercept) is given by $\beta_{1i}$, and the asymptote is $\beta_{0i} + \beta_{1i}$. Notice that when $\beta_{2i}$ is small, the curve may not reach the asymptote within a practical range of ages. The instantaneous growth rate is given by $df/dx = \beta_{1i}\beta_{2i} \exp(-\beta_{2i}x_{ij})$. Other parameterizations for the model are possible. We chose this particular nonlinear model, but there is no theoretical reason to choose one model over another. The monomolecular model fits the data well (Figs. 1 and 2), and we chose this model because the parameters have natural and easy interpretations. This is a nonlinear model and it requires nonlinear statistical methods (Seber & Wild, 1989).

Table 1. Models and fitted values for parameters of growth curves of ramus length of Western Arctic Herd caribou.

| Parameter | Parameter free | $\beta_{01} = \beta_{02}$ | $\beta_{11} = \beta_{12}$ | $\beta_{21} = \beta_{22}$ | $\sigma_1 = \sigma_2$ | $\beta_{11} = \beta_{12}$ $\beta_{21} = \beta_{22}$ |
|---|---|---|---|---|---|---|
| $\beta_{01}$ | 202.9 | 206.2 | 204.5 | 201.7 | 203.5 | 203.3 |
| $\beta_{11}$ | 84.52 | 81.70 | 82.71 | 84.32 | 83.84 | 81.59 |
| $\beta_{21}$ | 0.5675 | 0.5380 | 0.5612 | 0.6093 | 0.5628 | 0.6324 |
| $\sigma_1$ | 13.87 | 13.90 | 13.89 | 13.65 | 11.48 | 13.93 |
| $\beta_{02}$ | 224.2 | 206.2 | 218.1 | 227.8 | 223.1 | 220.4 |
| $\beta_{12}$ | 76.82 | 93.84 | 82.71 | 74.11 | 77.85 | 81.59 |
| $\beta_{22}$ | 0.6507 | 0.7571 | 0.6831 | 0.6093 | 0.6601 | 0.6324 |
| $\sigma_2$ | 9.34 | 9.40 | 9.36 | 9.51 | 11.48 | 9.37 |
| $2l(\theta \mid y)$ | 6014.93 | 6021.53 | 6015.80 | 6016.88 | 6094.91 | 6019.57 |
| AIC | 6030.93 | 6035.53 | 6029.80 | 6030.88 | 6108.91 | 6031.57 |

Because we wished to build a model of possibly two different curves, and to make decisions in model building, the full methodology is given here because it is not commonly used in wildlife analyses.

Fitting the model using maximum likelihood
Using equations (1) and (2), the negative log-likelihood then is,

$$l(\theta;y) = -\log[p(y;\theta)] \propto \sum_{i=1}^{2} \sum_{j=1}^{n_i} \log(\sigma_i) + \frac{1}{2\sigma^2_i}(Y_{ij} - f_i(x_{ij}))^2,$$

where $\theta = (\beta_{01}, \beta_{11}, \beta_{21}, \sigma_1, \beta_{02}, \beta_{12}, \beta_{22}, \sigma_2)$. Minimizing $l(\theta;y)$ for $\theta$ yields the maximum likelihood estimates. We programmed $l(\theta;y)$ using S-PLUS (Mathsoft Inc., Seattle WA.) and used the generic, derivative free minimization algorithm MS in S-PLUS to obtain the maximum likelihood estimates.

*Diagnostics*
The residuals from the fitted curve were formed by taking $Y_{ij} - f_i(x_{ij})$ for the fitted models. The residuals were plotted against $x_{ij}$ to look for any trend or inflation of variance in the residuals. Also, the residuals were tested to see if they were normally distributed (Shapiro & Wilk, 1965) using PROC UNIVARIATE in statistical software SAS (SAS Institute, Cary, NC).

*Likelihood ratio tests and AIC*
The most general model we can build is to have all free parameters that have separate estimates. This gives completely separate curves for the two time periods. However, we can consider simpler models (fewer estimated parameters) where we

set some elements in $\theta$ equal; for example, by assuming $\beta_{21} = \beta_{22}$. The simpler model is always a subset of the most general model, and we wish to decide whether to choose a simpler model or a more general one, and to test whether some parameters can be set equal.

*F*-tests and *t*-tests have been developed for linear models such as regression and ANOVA. For the nonlinear model that we are considering, we used the more general likelihood ratio test. The general theory of likelihood ratio tests can be found in most introductory texts on mathematical statistics (e.g., Bain & Engelhardt, 1987). In the context of model-building, a similar idea is to use Akaike Information Criteria (AIC; Akaike, 1973) to select the best model. AIC is defined to be,

AIC = $2l(\theta \mid y) + 2$ (number of estimated parameters).

The idea is to choose the model with the lowest AIC.

## Results
A series of 6 fitted models for the ramus length data is given in Table 1. The model with all free parameters (eight of them) is given in the first column. The second column shows the model with a common intercept, $\beta_{01} = \beta_{02}$, for both periods. Notice that the difference in $2l(\theta \mid y)$ for the two models is 6021.53 - 6014.93 = 6.60, and because this is greater than 3.84 ($P = 0.05$ for a chi-square with 1 degree of freedom), we can reject the null hypothesis that the two parameters are equal (i.e., that the curves have equal intercepts). However, notice the third column for the model, $\beta_{11} = \beta_{12}$. Here, the difference in $2l(\theta \mid y)$

Table 2. Models and fitted values for parameters of growth curves of diastema length of Western Arctic Herd caribou.

| Parameter | Parameter free | $\beta_{01} = \beta_{02}$ | $\beta_{11} = \beta_{22}$ | $\beta_{21} = \beta_{22}$ | $\sigma_1 = \sigma_2$ | $\beta_{11} = \beta_{22}$ $\beta_{21} = \beta_{22}$ |
|---|---|---|---|---|---|---|
| $\beta_{01}$ | 73.51 | 75.00 | 73.52 | 73.03 | 73.68 | 72.96 |
| $\beta_{11}$ | 40.73 | 40.54 | 41.24 | 40.17 | 40.84 | 40.65 |
| $\beta_{21}$ | 0.3455 | 0.3120 | 0.3345 | 0.3716 | 0.3394 | 0.3637 |
| $\sigma_1$ | 7.608 | 7.608 | 7.618 | 7.605 | 6.675 | 7.603 |
| $\beta_{02}$ | 84.76 | 75.00 | 86.80 | 87.46 | 85.10 | 88.40 |
| $\beta_{22}$ | 43.22 | 51.25 | 41.24 | 41.52 | 42.90 | 40.65 |
| $\beta_{22}$ | 0.4121 | 0.5224 | 0.3969 | 0.3716 | 0.4098 | 0.3637 |
| $\sigma_2$ | 5.919 | 5.938 | 5.893 | 5.908 | 6.675 | 5.910 |
| $2l(\theta \mid \mathbf{y})$ | 4936.82 | 4944.04 | 4937.19 | 4937.78 | 4969.46 | 4937.95 |
| AIC | 4952.82 | 4958.04 | 4951.19 | 4951.78 | 4983.46 | 4949.95 |

for the two models is $6015.80 - 6014.93 = 0.87$, and because this is less than 3.84, we cannot reject the null hypothesis that the two parameters are equal (i.e., that the amount of growth was equal). Likewise, we cannot reject the null hypothesis $\beta_{21} = \beta_{22}$, that the growth rate was equal. However, it is clear the variances are not equal for the two groups, with the earlier period having higher variability. A final step is to consider whether both $\beta_{11} = \beta_{12}$ and $\beta_{21} = \beta_{22}$. The final column in Table 1 shows the difference in $2l(\theta \mid \mathbf{y})$ for the model in column 1 versus the model in column 6, which is $6019.57 - 6014.93 = 4.64$, and because this is less than 5.99 ($P = 0.05$ for a chi-square with 2 degrees of freedom), we cannot reject the null hypothesis that both sets of parameters are equal. Finally, note that the model with the lowest AIC is the model where $\beta_{11} = \beta_{12}$, so according to AIC this is the best overall model. We also did diagnostics. For the model where both $\beta_{11} = \beta_{12}$ and $\beta_{11} = \beta_{12}$, the residuals showed no pattern with age and they could not be rejected as coming from a normal distribution ($P = 0.62$, $n = 438$ for the 1960s period; $P = 0.54$, $n = 598$ for the 1980s period). Fig. 1 shows the fitted model where both $\beta_{11} = \beta_{12}$ and $\beta_{21} = \beta_{22}$.

The results for diastema are given in Table 2, and the conclusions are very similar as for those in Table 1. Again, we cannot reject the model that both $\beta_{11} = \beta_{12}$ and $\beta_{21} = \beta_{22}$, and in contrast to Table 1, this is also the best model using AIC. For diagnostics, the residuals showed no pattern with age, and they also could not be rejected as coming from a normal distribution ($P = 0.98$, $n = 438$ for the 1960s group; $P = 0.93$, $n = 598$ for the 1980s group). Fig. 2 shows the fitted model where both $\beta_{12}$ and $\beta_{21} = \beta_{22}$.
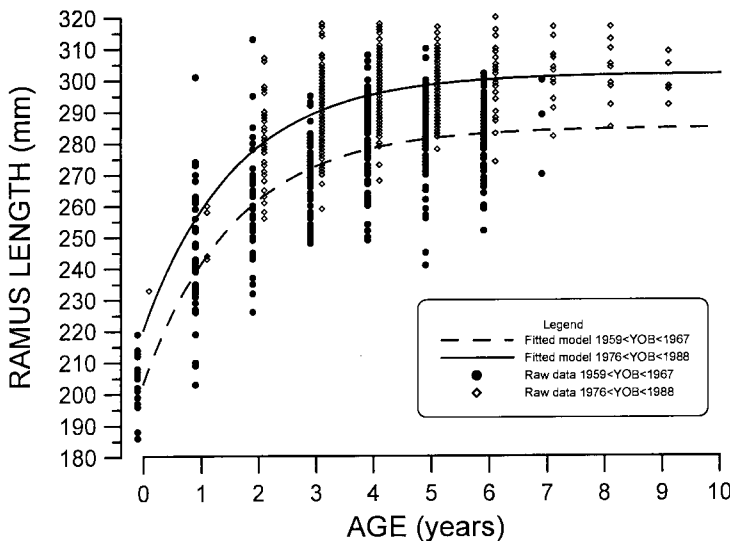


Fig. 1. Fitted models of growth curves for ramus length from two collections of mandibles of male caribou from the Western Arctic caribou herd.

## Discussion

We infer from the models developed here that growth was suboptimal during the period of population decline in the 1960s and early 1970s, probably because
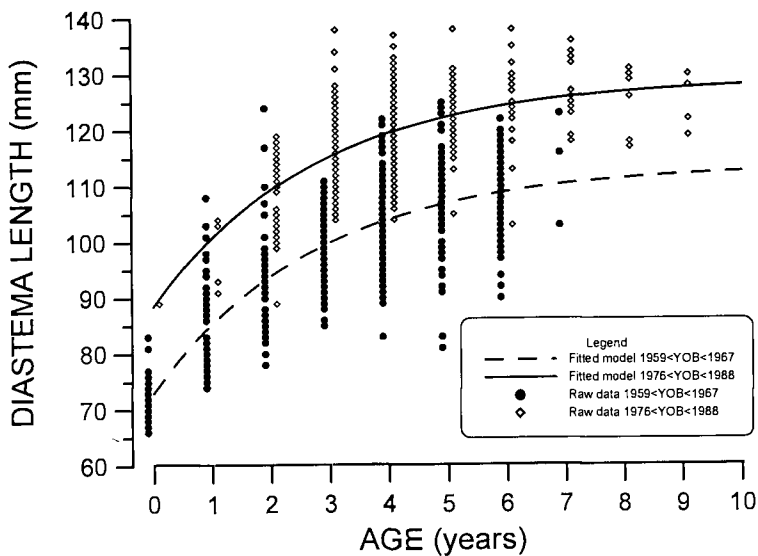
caribou during the later collection, and the difference in body size between periods was more related to long-term weather. Doerr (1979: 239) expressed this opinion when he found differences in mandible size from 2 smaller collections in the late 1950s when herd size was presumably not changing greatly. A full discussion of these factors is well beyond the scope of this paper. However, it is clear that caribou in the Western Arctic Herd went through a period of reduced body size associated with a population decline in the late 1960s and early 1970s, and subsequently increased in population size and body size (Figs. 1 and 2).

calves were smaller after their first summer, and did not compensate in subsequent years. That is, we cannot reject the hypothesis that the curves differ only in their intercepts. Some compensatory growth may have occurred (e.g., notice $\beta_{1i}$ in Table 1) but it was not significant. Small samples of calves and yearlings (age classes 0 and 1) in the 1980s collection reduced the predictive power of the model for these classes. The smaller size of caribou during periods of high population density and lack of significant compensatory growth is consistent with previously analyzed data for Alaskan caribou (Valkenburg et al., 1991; Eberhardt & Pitcher, 1992), and wild reindeer in Norway (Reimers et al., 1983; Skogland, 1983, 1984, 1989, 1990; Eloranta & Nieminen, 1986; Reimers, 1997). The data presented do not allow us to determine whether smaller body sizes in the 1960s resulted from poorer nutrition due to population density or unfavorable weather. The fact that the population size was larger in the latter half of the 1977 to 1989 sampling period than in the 1960s makes interpretation based on population density difficult. However, in the later collection, there were only 5 caribou mandibles from age classes 0 and 1, so that most of the caribou represented in this collection grew up prior to 1987 when the herd size was still relatively low. Additionally, time lag effects with resources complicate the issue. It is also possible that weather was more favorable for body growth in

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